Functional diversity underlies demographic responses to environmental variation across European forests

Journal:	*Global Ecology and Biogeography*
Manuscript ID	GEB-2015-0452.R2
Manuscript Type:	Research Papers
Date Submitted by the Author:	n/a
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Keywords:	boreal biome, climate warming, forest succession, FunDivEUROPE, growth, Mediterranean biome, mortality, plant functional traits, regeneration, temperate biome

Functional diversity underlies demographic responses to environmental variation in European forests

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Keywords: boreal biome, climate warming, forest succession, FunDivEUROPE, growth, Mediterranean biome, mortality, plant functional traits, recruitment, temperate biome.

Short running title: Tree diversity and demography in European forests

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Number of words in abstract: 294

Number of words in main body (from the Introduction to discussion): 4996

Number of references: 50

Abstract

Aim Biodiversity loss and climate-driven ecosystem modification is leading to substantial changes in forest structure and function. However, diversity effects on demographic responses to the environment are poorly understood. We tested the diversity hypothesis (measured through functional diversity) and the mass-ratio hypothesis (measured through functional identity) on tree growth, tree mortality and sapling abundance. We sought to determine whether functional diversity underlies demographic responses to environmental variation in European forests.

Location Europe (Spain, Germany, Wallonia, Finland and Sweden).

Methods We used data from five European National Forest Inventories from boreal to the Mediterranean biomes (*c.* 700,000 trees in 54,000 plots and 143 tree species) and the main forest types across Europe (i.e. from needle-leaved evergreen forests to broad-leaved deciduous forests). For each forest type, we applied maximum likelihood techniques to quantify the relative importance of stand structure, climate and diversity (i.e. functional diversity and functional identity) as determinants of growth, mortality and sapling abundance. We also tested whether demographic responses to environmental conditions (including stand density, evapotranspiration and temperature anomalies) varied with functional diversity.

Results Our results suggest that functional diversity had a positive effect on sapling abundance and growth rates in forests across Europe, while no effect was observed for tree mortality. Functional identity had a strong effect on mortality and sapling abundance, with greater mortality rates in forests dominated by needle-leaved individuals and greater abundance of saplings in forests dominated by broad-leaved individuals. Furthermore, we observed that functional diversity modified stand density effects on demographic responses in Mediterranean forests and the influence of evapotranspiration and temperature anomalies in forests widely distributed across Europe.

Main conclusion Our results suggest that functional diversity may play a key role in forest dynamics through complementarity mechanisms, as well as by modulating demographic responses to environmental variation.

INTRODUCTION

Forests provide multiple ecosystem functions and services fundamental to human well-being (e.g. Gamfeldt *et al.*, 2013). However, forests are complex ecosystems dominated by long-lived species of large size and often limited dispersal ability that face major challenges due to diversity loss and rapid climate change (e.g. Jump & Peñuelas, 2005). Diversity loss is leading to important changes in the functioning of multiple ecosystems, similar in magnitude to other global change drivers (e.g. Tilman *et al.*, 2012). In addition, climate change is altering basic demographic responses of tree species, from increases in drought-induced tree mortality events to reductions in recruitment and growth (e.g. Settelle *et al.,* 2014; Allen *et al.*, 2015).

Two main hypotheses have been proposed to explain the underlying influence of plant functional traits on forest functioning: (i) the diversity hypothesis, which states that functionally-different species can coexist due to complementarity mechanisms which can lead to higher levels of forest functioning; and (ii) Grime's mass ratio hypothesis, which states that the functional traits of dominant species in a community most influence the level of ecosystem functioning (e.g. Grime, 1998; Mokany *et al.*, 2008). Most biodiversity and ecosystem functioning studies in forests have focused on tree growth (e.g. Morin *et al.*, 2011; Ruiz-Benito *et al.*, 2014a). However, Liang *et al.* (2007) observed that diversity effects could be even larger for recruitment than for growth in conifer forests. In addition, Lasky *et al.* (2014) found that the magnitude of diversity effects on biomass changes was larger in early-successional than late-successional tropical forests, due to differences in mortality and growth patterns between the stages. Despite growing evidence of functional diversity and identity effects on tree growth in forest from boreal to Mediterranean climates, it is not clear whether diversity effects are as important for other demographic processes such as recruitment and

mortality. Furthermore, there is increasing evidence that diversity effects on growth may be modulated by other factors such as climatic conditions (Jucker *et al.*, 2015; Toïgo *et al.*, 2015).

Recent climate change includes temperature increases (i.e. from warmer summers in the Mediterranean to warmer winters in boreal regions) and more frequent and intense droughts that are leading to mortality events (Allen *et al.*, 2015) and reductions in recruitment (Walck *et al.*, 2011). Interactions between climate and stand structure are altering demographic patterns and decreasing biomass accumulation rates in ecosystems with low water availability (Ruiz-Benito *et al.*, 2014b). The alteration in demographic responses may result in changes of the distributional range of species under climate change (e.g. Benito-Garzón *et al.*, 2013). Mortality responses to climate have been shown to largely depend on stand structure (Ruiz-Benito *et al.*, 2013), meanwhile recruitment patterns are essential determinants of future community composition and structure (Carnicer *et al.*, 2014). During the last decade there has been intense debate over the importance of diversity effects on forest functioning, yet these studies have mainly focused on species richness and tree growth as a key ecosystem function (e.g. Zhang *et al.*, 2012; Vilà *et al.*, 2013). Two recent studies suggest that complementarity mechanisms in forest functioning could be more important in resource-limited forests such as Mediterranean drought-prone forests (Grossiord *et al.*, 2014b; Jucker *et al.*, 2015). However, the potential effect of diversity on multiple demographic responses to abiotic and biotic environment remains poorly understood.

We used five National Forest Inventories with more than 55,000 plots covering Mediterranean to temperate and boreal biomes, and including the main forest types across Europe (i.e. broad-leaved vs. needle-leaved and evergreen vs. deciduous forests, see Fig. 1 and Baeten *et al.*, 2013). We collated data on four key traits for plant performance for the 143 species (i.e. leaf mass per area, wood density, maximum tree height and seed mass, e.g. Díaz

et al., 2016) and tested the influence of functional composition on demography, following: (i) the diversity hypothesis, i.e. functional diversity determined growth and recruitment through complementarity mechanisms (particularly in water-limited Mediterranean forests) and ameliorated the negative effects of environment (i.e. including competition, climate and recent climate warming) on demography; and (ii) the mass ratio hypothesis, i.e. functional identity influences demographic patterns due to dominance of certain functional traits through selection mechanisms, particularly between contrasting life history strategies. To test these hypotheses, we quantified the functional composition of each plot as the absolute effect of functional diversity (measured as the dispersion of key traits in each plot) and functional identity (measured as the community weighted mean of a single trait in each plot) on growth, mortality and sapling abundance. Secondly, we explored whether demographic responses to biotic and abiotic environmental conditions (i.e. including competition, climate and recent temperature increases) were modified by functional diversity.

METHODS

Forest inventory dataset and demographic variables

We compiled data from the National Forest Inventories (NFIs) of Spain, Germany, Belgium (Wallonia), Sweden and Finland (see Appendix S1 and Table S1 in Supporting Information). For each tree we compiled information regarding the species name (see Table S2), diameter at breast height (d.b.h., mm) and status (alive or dead). We classified each plot based on the abundance of the species in the following classifications: (i) leaf characteristics (i.e. broad- vs. needle-leaved, deciduous vs. evergreen), and (ii) Mediterranean distribution (i.e. distribution only occurs in the Mediterranean climate, see Table S1), because the response to climate and, therefore, the strength of diversity effects may be different in forests well adapted to extreme climatic conditions (Grossiord *et al.*, 2014a,b). We only considered forest types with more than 1,000 plots, resulting in 52,180 plots in the following forest types: broad-leaved deciduous, Mediterranean broad-leaved evergreen, Mediterranean needle-leaved evergreen forests and other needle-leaved evergreen forests (see Fig. 1 and Table 1).

As demographic variables we used (see also Appendix S2): (i) tree growth ($cm^2\ ha^{-1}\ yr^{-1}$) calculated as the annual sum of the basal area increment of adult trees that survived both censuses and new adult trees in the second census (i.e. d.b.h. > 10 cm and height > 130 cm); and (ii) tree mortality ($cm^2\ ha^{-1}\ yr^{-1}$) calculated as the annual basal area of adult trees lost between consecutive inventories, and (iii) sapling abundance (No. saplings ha^{-1}) calculated as the abundance of individuals with a height between 30 cm and 130 cm in the second census of the consecutive inventories (see Table S1 and Fig. S1).

Abiotic and biotic determinants of demographic responses

Initially, we selected 27 potential climatic variables based on temperature and precipitation which describe the: (i) spatial climatic variability over the period 1950-2000 (WorldClim, CGIAR-CSI GeoPortal, and SPEIbase v2.2.; see a list of data sources in Appendix 1 and Table S3); and (ii) recent climate change (NOAA, Boulder, Colorado, USA) defined as the differences in temperature or precipitation between the study period (i.e. the number of years between the two consecutive inventories plus two years before the first survey) and the mean value for the reference period (1900-2010).

Stand structure (i.e. stand tree density calculated as the number of trees per hectare, and mean d.b.h. calculated as the mean diameter of all trees in the stand) and community functional composition (i.e. functional diversity and identity) were also estimated for each plot. We used four key traits to describe the functional composition (see Table S4 and a list of trait data used can be found in Appendix 1): maximum tree height (m), wood density (g cm^{-3}), seed mass (mg) and leaf mass per area (g m^{-2}). These traits are widely recognised as key traits of plant function and performance: maximum height, wood density and seed mass are closely related to life history strategy, while leaf mass per area is related to resource acquisition and plant growth strategy (e.g. Paquette & Messier, 2011; Swenson *et al.*, 2012). Functional diversity (FD, Laliberté & Legendre, 2010) was calculated as the dispersion of functional traits in each plot based on all traits and only seed mass, wood density and maximum height (see Appendix S2). Functional identity (FI, Lavorel *et al.*, 2008) was calculated as the community-level weighted mean of each trait in each plot.

Prior to parameterising our maximum likelihood models of demographic responses, we performed a variable selection from the available climatic and biotic variables (Fig. S2-S3). To select from the large climatic dataset we performed a PCA and we selected potential evapotranspiration (PET, mm) as representative of spatial climatic variability (highly and

negatively correlated with the first axis of the PCA explaining 49.9% of the variance) and temperature anomaly (TA, ºC) as representative of recent climate change (TA showed a stronger negative correlation with the first axis of the PCA than precipitation anomaly). To represent stand structure, we selected tree density (Density, No. trees ha^{-1}) and mean tree diameter (Size, mm) to account for stand density and developmental stage. We selected functional diversity based on seed mass, wood density, and maximum height, and FI based on leaf mass per area (hereafter FI_{LMA}). The FD index was selected because the correlation between all diversity indices was high (i.e. considering all traits or subset of traits, $r > 0.85$) and the subset of traits including seed mass, wood density and maximum tree height has been previously identified as a good predictor of forest functioning (the same indices were used in Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014a) and competitive outcomes (Kunstler *et al.*, 2016). The FI index selected was based on leaf mass per area it has been identified as a good indicator of contrasting life history strategies and it is different for the dominant species in the forest types (see Fig. S3, e.g. Wright *et al.*, 2004).

Maximum likelihood analysis of tree growth, tree mortality and sapling abundance

We fitted non-linear models for tree growth ($cm^2\ ha^{-1}\ yr^{-1}$), tree mortality ($cm^2\ ha^{-1}\ yr^{-1}$) and abundance of saplings (No. saplings ha^{-1}) for each forest type separately. The predicted demographic responses (μ_i) were modelled using the following non-linear model:

$$\mu_i = \mu_{pot} \times \text{Climate effect} \times \text{Structural effect} \times \text{Functional composition effect} \quad (1)$$

where μ_{pot} is an estimated model parameter that represents the maximum potential value of tree growth, tree mortality or sapling abundance when all the predictors are at their optimal values; i.e. the potential predictor are sets of non-linear terms that contain scalar modifiers ranging from 0 to 1 that quantify the influence of (ii) climatic conditions (i.e. *climate effect*: PET and TA; Eqn. (2)); (iii) stand structure (i.e. *structural effect*: density and size; defined in Eqn. (3)); and (iv) functional composition (i.e. *functional composition effect*: FD and FI_{LMA}; defined in Eqn. (4)).

For the climate and structural effect, we selected a Gaussian function because it is flexible enough to allow for typical hump-shaped species-environment relationships of species to environment, but also allows for monotonic or sigmoidal responses within restricted ranges of either axis (Gómez-Aparicio *et al.* 2011; Ruiz-Benito *et al.* 2014a). Thus, the *climate effect* on demographic responses was modelled using a Gaussian functional form:

$$\text{Climate effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{PET}-\text{XPET}_a}{\text{XPET}_b}\right)^2\right] \times \exp\left[-\frac{1}{2}\left(\frac{\text{TA}-\text{XTA}_a}{\text{XTA}_b}\right)^2\right] \quad (2)$$

where the parameters $XPET_a$ and XTA_a represent the PET and TA at which maximum tree growth occurs, and $XPET_b$ and XTA_b are the parameters that control the variance of the normal distribution (i.e. the breadth of the function). The *structural effect* on demographic responses was modelled using a bivariate Gaussian function:

$$\text{Structural effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{Density}-\text{XSTD}_a}{\text{XSTD}_b}\right)^2\right] \times \exp\left[-\frac{1}{2}\left(\frac{\text{Size}-\text{XS}_a}{\text{XS}_b}\right)^2\right] \quad (3)$$

where the density effect is measured in terms of stand tree density (No. trees ha^{-1}) and the size effect is measured through stand mean d.b.h. (mm). $XSTD_a$ and XS_a are the density

and size, at which maximum growth occurs, and $XSTD_b$ and XS_b are the estimated parameters that control the breadth of the function.

For tree growth and sapling abundance, the influence of functional diversity (FD) was modelled using a variation of the exponential form, because FD can have a positive effect on demographic responses at low values of FD but later can reach an asymptotic level (e.g. Paquette and Messier, 2011; Ruiz-Benito *et al.*, 2014a). Functional identity (FI_{LMA}) was modelled using a Gaussian function because it is flexible enough to allow for the quadratic and monotonic responses of forest performance along functional identity gradients (e.g. Ruiz-Benito *et al.*, 2014a). Thus, the *community functional composition effect* was modelled following the next functional form:

$$\text{Functional composition effect} = [1 - \exp((\text{XFD}_\text{a} \times \text{FD}) - \text{XFD}_\text{b})] \times \exp\left[-\frac{1}{2}\left(\frac{\text{FI}_{LMA} - \text{XFI}_\text{a}}{\text{XFI}_\text{b}}\right)^2\right] \quad (4)$$

where the parameter XFD_a determines the shape of the effect of FD on the predicted variable and XFD_b defines the intercept of the function. The parameter XFI_a represents the FI_{LMA} value at which maximum tree growth and sapling abundance occurs, and XFI_b determines the breadth of the function. For stand mortality, we considered that FD could reduce mortality rates and, thus, we used a variant of Eqn. (4) where the FD was in this case modelled using a negative exponential form:

$$\text{Functional composition effect} = [\exp((\text{XFD}_\text{a} \times \text{FD}) - \text{XFD}_\text{b})] \times \exp\left[-\frac{1}{2}\left(\frac{\text{FI}_{LMA} - \text{XFI}_\text{a}}{\text{XFI}_\text{b}}\right)^2\right] \quad (5)$$

where the parameter XFD_a determines the shape of the effect of FD on the predicted variable and XFD_b defines the intercept of the function.

The indirect effects of FD on the demographic responses to environmental conditions were tested through variants of parameters X_b in Eqns. (2) and (3). To this aim, we modified the expression that was used to obtain the fitted parameters X_b that control the breadth of the function and, therefore, determine the strength of the environmental effect on demography. The parameters X_b which determine the strength of the environmental effect on demography (i.e. parameters $XSTD_b$, $XPET_b$ and XTA_b; relating to density, PET and TA effects on demographic responses, respectively) were allowed to vary as a function of functional diversity following:

$$X_b = \beta \times FD + X_b' \quad (6)$$

where β is a parameter that indicates how FD modifies demographic responses to environment. β = 0 reflects no influence of FD on demographic responses to environmental conditions. As we hypothesised larger demographic responses to environment when FD is low, β > 0 was allowed for tree growth and sapling abundance and β < 0 was allowed for tree mortality (i.e. at high FD there is a reduced influence of density, PET and/or TA on tree growth, tree mortality and/or sapling abundance responses).

Parameter estimation, model selection and validation

We fitted separate non-linear models of tree growth, tree mortality and sapling abundance for each forest type. To select the best model, we followed the principle of parsimony and used two-units difference in Akaike Information Criterion as a support interval to assess the strength of evidence of individual maximum likelihood parameter estimates, being roughly equivalent to the 95% support limit defined using a likelihood ratio test (Burnham &

Anderson, 2002). Thus, the full model was compared with models that ignored the effect of each predictor variable (i.e. not including the effect of PET, TA, density, size, FD and FI_{LMA}, respectively in each model) which also informed about the strength of the evidence for including each variable in the final model.

Given the high number of zeros in the tree mortality and sapling abundance data (see Table 1) a zero inflated normal distribution (ZIN) and a negative binomial distribution were used, respectively, while a normal error distribution was used for tree growth (see Fig. S5). For tree mortality our statistical model estimates two components simultaneously: (i) the probability of mortality based on the binomial variable related to stand mortality, and (ii) the predicted basal area lost due to mortality in the plots that experienced mortality. The ZIN function has the following functional form:

$$Prob(Y = y_i) = \begin{cases} p_s & if\ y_i = 0 \\ (1 - p_s)Normal(y_i|\theta) & if\ y_i > 0 \end{cases} \quad (8)$$

Where y_i represents the basal area lost due to natural mortality in plot i, p_s represents a constant probability across the data set of getting zero mortality. When $y_i > 0$ stand mortality was modelled using a normal distribution given the data y_i and the parameters θ, obtained from structural, climatic and diversity effects following Eqns. (1)-(5).

The parameter estimates provide the basis for determining the magnitude of the influence of a given process, with maximum likelihood estimates of parameter values close to zero or confidence intervals overlapping zero indicating no effect. We used simulated annealing optimisation procedures to determine the parameters that maximize the log-likelihood of observing tree growth, mortality and recruitment (Goffe *et al.*, 1994). As a measure of the goodness of fit we calculated the R^2 of the non linear models fitted (1 - SSE/SST, SSE: sum of squares error, SST: sum of squares total). As a measure of bias in the

prediction we plotted the observed and predicted data and we calculated the slope of the regression with a zero intercept, where an unbiased model should have a slope of the regression equal to 1 (i.e. line 1:1). In addition, we checked the influence of census interval using similar approaches to Chen & Luo (2015) (see Appendix S2). The analyses were performed using the likelihood package 1.6 (Murphy, 2012) in R.2.15 (R Core Team, 2012).

RESULTS

Climatic, structural and functional composition influence on tree growth

The most parsimonious models for tree growth in Mediterranean evergreen forests (both needle- and broad-leaved forests) included variables related to climate, stand structure and functional composition (Table 2). However, in forests broadly distributed throughout Europe functional composition was not strongly supported in the final model (i.e. broad-leaved deciduous and other needle-leaved forests, see ΔAIC in Table 2). Tree growth responses to stand structure were stronger than those observed for climate (see the largest increase in AIC when stand structure effect was dropped from the full models, Table 2). All of the models produced unbiased estimates of tree growth (i.e. slopes of predicted versus observed values were all close to 1) and the explained variance (R^2) ranged from 43% for broad-leaved deciduous forests to 54% for other needle-leaved evergreen forests (Table 2).

Functional diversity and identity were particularly important determinants of tree growth in Mediterranean needle-leaved evergreen forests followed by Mediterranean broad-leaved evergreen forests (see Table 2). Tree growth increased slightly with functional diversity in all forest types (Fig. 2a), and strongly with functional identity based on leaf mass per area in Mediterranean needle-leaved evergreen forests (Fig. 2b). Functional diversity also indirectly modified tree growth responses to stand tree density in Mediterranean forests (see Table 2 and Fig. 3a) and to potential evapotranspiration in broad-leaved deciduous forests (Table 2 and Fig. 3b). Functionally diverse forests experienced lower effects on demography of the extremes of density or potential evapotranspiration.

Climatic, structural and functional composition influence on tree mortality

The final mortality models included variables related to climate (potential evapotranspiration and temperature anomalies), stand structure (i.e. stand basal area and mean d.b.h.) and functional identity (Table 2). The influence of stand structure on mortality was larger than climate and functional identity (see ΔAIC in Table 2). All of the models produced unbiased estimates of tree mortality and explained variance (R^2) ranged from 11% for broad-leaved deciduous forests to 34% for Mediterranean needle-leaved evergreen forests (Table 2).

Tree mortality was not influenced by functional diversity (see ΔAIC < 2 when FD was removed from the full model in Table 2), whilst functional identity, based on leaf mass per area, had a strong influence, with a relative importance similar to that of potential evapotranspiration (Table 2). We observed maximum stand mortality towards high values of leaf mass per area (i.e. forests dominated by needle-leaved species, see Fig. 2c). Our results suggest that mortality responses to environmental conditions could vary depending on functional diversity in needle-leaved and broad-leaved deciduous forests (see β parameters in Table 2). The positive relationship between stand tree density and tree mortality was lower in more diverse Mediterranean needle-leaved forests (see Fig. 3c). Furthermore, functional diversity reduced the influence of potential evapotranspiration on tree mortality in broad-leaved deciduous and other needle-leaved evergreen forests, and temperature anomalies in Mediterranean and other needle-leaved evergreen forests (Fig. 3a).

Climatic, structural and functional composition influence on sapling abundance

Climate variables were particularly important for determining sapling abundance patterns in all forest types, followed by functional composition and stand structure variables, although mean d.b.h. in broad-leaved deciduous forests and stand tree density in Mediterranean

needle-leaved evergreen forests were not supported in the most parsimonious model (ΔAIC in Table 2). All of the models produced unbiased estimates of sapling abundance and explained variance ranged from 9% for Mediterranean needle-leaved evergreen forests to 25% for other needle-leaved evergreen forests (Table 2).

The abundance of saplings was strongly influenced by functional diversity and identity, with a comparable importance to temperature anomaly and stand structure (see strength of evidence through ΔAIC in Table 2). Sapling abundance increased with functional diversity, particularly in evergreen forests (Fig. 2b). Maximum sapling abundance occurred at low values of functional identity based on leaf mass per area (i.e. stands dominated by broad-leaved species), except in needle-leaved evergreen forests broadly distributed in Europe (Fig. 2e). Functional diversity generally did not cause modification of sapling abundance responses to environmental conditions (see Table 3). In other needle-leaved evergreen forests broadly distributed across Europe, however, high tree diversity reduced sapling abundance responses to potential evapotranspiration and temperature anomaly (Fig. 3a,b).

DISCUSSION

Demographic responses to functional diversity

Our results suggest that functional diversity could directly influence tree growth and sapling abundance, while it was not supported for mortality responses. The enhanced tree growth observed with functional diversity is congruent with previous studies that found a positive effect of species richness on wood production across European forests (Vilà *et al.*, 2013), and particularly those suggesting a large effect of diversity in Mediterranean forests (Ratcliffe *et al.*, 2016; Ruiz-Benito *et al.*, 2014a). The influence of diversity on demography could be due to complementarity mechanisms, which can be particularly strong in water-limited Mediterranean forests. As a proxy of potential complementarity effects, we used functional diversity based on wood density, maximum tree height and seed mass. These traits have been identified as key for plant performance and indicators of life history strategies (Hooper *et al.*, 2005; Swenson *et al.*, 2012). Increases in functional diversity could be due to increases in the presence of individuals with contrasting functional traits (e.g. pine-oak mixed forests), which are particularly frequent in the Mediterranean and suggest niche partitioning is a plausible explanation of the positive effect of diversity in Mediterranean water-limited forests (Poorter *et al.*, 2012; Carnicer *et al.*, 2013).

Our results support the existence of a positive relationship between functional diversity and sapling abundance in all the forest types studied (Table 2), suggesting that complementarity mechanisms may be driven by niche partitioning and facilitation processes. In addition, congruent with other studies (see Liang *et al.* 2007), we found tree diversity to have a greater influence on sapling abundance than tree growth or mortality (Fig. 2). Sapling abundance in broadleaved deciduous forests was relatively unresponsive to functional

diversity, but greater sapling abundance was observed in conifer-dominated and Mediterranean broad-leaved forests (Fig. 2). The strong demographic responses observed in conifer forests suggest that the abundance of saplings is favoured when there is a coexistence of functionally diverse species, which ultimately depends on climate, management and land use history (e.g. pine-oak dominance in the Mediterranean region, Zavala & Zea, 2004; Sheffer, 2012). The successional status was not available from all the inventories, however, we controlled for stand-structure (i.e. including density and size related effects), and the forest-type classification used is related to the general successional status of different species and their coexistence. Thus, further increments in functional diversity may be due to changes in the successional status with an increasing number of species and functional groups, which could lead to higher recruitment success promoting facilitation (Zavala *et al.*, 2011).

Demographic responses to functional identity

We observed the greatest mortality rates at high levels of leaf mass per area (i.e. stands dominated by needle-leaved species), but the highest abundance of saplings occurred at low values of leaf mass per area (i.e. stands dominated by broad-leaved species, see Fig. 2). These results suggest that stands with a large proportion of conifers experienced the greatest mortality rates, as has been already observed at large spatial scales (e.g. Ruiz-Benito *et al.*, 2013). A possible explanation is that needle-leaved species have generally shorter life spans than broad-leaved species and are less shade-tolerant (Poorter *et al.*, 2012). Moreover, conifers have been often planted at high densities, which could underlie the low abundance of saplings and high mortality rates (e.g. Ruiz-Benito *et al.*, 2012, 2013). In addition, our results suggest that stands dominated by broad-leaved species experience larger abundances of saplings in all the forest types studied (see Fig. 2 and Table 1, see also Vayreda *et al.*, 2013).

An exception was found for conifers widely distributed in Europe, which showed higher abundance of saplings in stands dominated by conifers rather than broad-leaved species. These are forests dominated by *Pinus sylvestris* and *Pinus nigra*, which can constitute successional end-points under severe environmental conditions, such as cold climates at high altitude or shallow and rocky soils (e.g. Zavala & Zea, 2004).

Altogether, our results suggest that some Mediterranean needle-leaved forests may be experiencing the most important changes in species dominance because of the high mortality in conifer dominated stands and the high abundance of saplings observed in broadleaved dominated forests (Fig. 2). This may lead to increased dominance of oak species, which agrees with previous studies that found a severe limitation in recruitment for *Pinus* species, and an expansion in *Quercus* species recruitment (Carnicer *et al.*, 2014). Furthermore, we found climate and functional identity to be more important for the abundance of saplings than stand structure in all forest types studied (Table 2). This finding may be due to the large climatic gradient covered and the influence of functional identity, which might reflect a successional trajectory along large climatic gradients (e.g. Ratcliffe *et al.*, 2016). These results are congruent with the observed increase in sapling abundance in broad-leaved forests and increase in mortality rates in needle-leaved forests. Yet, further studies seeking the underlying drivers of multiple demographic processes and their effects on forest composition are needed to better understand the direction and conditions for changes in vegetation.

Functional diversity underpins demographic responses to environmental conditions

Our models provide evidence of different demographic responses to tree density depending on the diversity of Meditteranean forests (see Table 2), with a smaller effect of extreme tree densities on growth and mortality in more diverse forests (see Fig. 3). At high stand density

increased mortality and decreased growth has been observed in European forests, probably due to high levels of competition for resources (Gómez-Aparicio *et al.*, 2011; Ruiz-Benito *et al.*, 2013). At low densities a combination of competition for limiting resources and a greater exposure might boost interactions between climate and stand structure (e.g. Ruiz-Benito *et al.*, 2014b). Our result is consistent with previous studies that found that the positive effect of species richness on productivity was mediated by stand basal area (see Vilà *et al.*, 2013) and water availability (Pretzsch *et al.*, 2016). The trend observed suggests that diverse stands are able to pack more densely without showing strong declines in growth or increased mortality, which could be due to greater crown plasticity in mixed-species forests (see also Jucker *et al.*, 2015). Furthermore, our finding agrees with studies that found a strong effect of diversity promoting water use efficiency in drought prone environments (Grossiord *et al.*, 2014b; Jucker *et al.*, 2016), this mechanism would be particularly important at high densities in Mediterranean forests.

We also found support for an effect of functional diversity ameliorating the negative effect of climate (i.e. potential evapotranspiration) and recent warming (i.e. temperature anomalies) on tree mortality and sapling abundance in some forests (see Table 2). These forests are widely distributed across Europe (i.e. broad-leaved deciduous and other needle-leaved evergreen forests) covering Mediterranean to boreal biomes (Fig. 1) and, therefore, experiencing a large gradient in potential evapotranspiration and temperature anomalies (see Fig. S2). We observed that tree diversity may modify demographic responses at the extremes of potential evapotranspiration and recent climate warming was particularly important for coniferous forests dominated by *Pinus sylvestris* and *Pinus nigra* species. A large impact of climate change has been predicted on the demography and distribution of these species, particularly in mesic climates and rear edge distributions (Benito-Garzón *et al.*, 2013; Carnicer *et al.*, 2014). Relatively low biomass increments have been reported in

Mediterranean and boreal forests due to the effect of both water availability and minimum temperatures (Ruiz-Benito *et al.*, 2014b). Thus, diversity modification of demographic responses to extreme climates may be particularly important in these forests where large impacts of increased temperature and reduced water availability are expected (e.g. Frank *et al.*, 2015).

Potential implications of diversity loss and species dominance under changing climate

Altogether our results support the diversity hypothesis, suggesting that complementarity mechanisms play a key role in forest dynamics, in addition to previous studies that mainly focused on productivity or biomass (see e.g. Morin *et al.,* 2011; Ruiz-Benito *et al.*, 2014a). The importance of tree diversity for the functioning of European forests could have been underestimated as we show that it can affect multiple demographic processes, including demographic responses to environmental conditions across Europe. We observed larger growth rates and sapling abundance in more functionally diverse forests across all European forests. Furthermore, the indirect effects of functional diversity on demographic responses to environmental variation supported in our model results also highlight the crucial task of maintaining functionally diverse forests. Here, we used growth and mortality rates based on basal area dynamics instead of biomass since basal area is a reliable proxy of biomass (e.g. Slick *et al.*, 2010), although further studies based on biomass may provide additional indications of effects of functional diversity on plant performance through complementarity mechanisms.

The influence of functional identity on demographic processes confirms the importance of the mass ratio hypothesis (i.e. dominance of species and contrasting functional groups). The variation in mortality and sapling abundance responses along functional identity

gradients in Mediterranean pine forests suggests that forest dynamics could lead to a higher dominance of broad-leaved species in these forests. Our results highlight the importance of further studies seeking to better understand underlying drivers and mechanisms of regional changes in forest dominance, particularly understanding mechanisms of species coexistence and diversity maintenance under a changing environment at large-spatial scales.

ACKNOWLEDGEMENTS

The research leading to these results has received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement No. 265171 (FunDivEUROPE) and No PCOFUND-GA-2010-267243 (Plant Fellows), The Leverhulme Trust (No. IN-2013-004), The University of Stirling, and MINECO (FUNDIVER, No. CGL2015-69186-C2-2-R). We thank anonymous referees for their constructive comments on previous versions of this article, and the MAGRAMA for access to the Spanish NFI, the Johann Heinrich von Thünen-Institut for access to the German NFI, the Natural Resources Institute Finland (Luke) for making permanent sample plot data available, the Swedish University of Agricultural Sciences for making the Swedish NFI data available, and Hugues Lecomte for access to the Walloon NFI. The study has been supported by the TRY initiative on plant traits (http://www.try-db.org). TRY is hosted and developed at the Max Planck Institute from Biochemistry, and supported from DIVERSITAS and iDiv.

Biosketch

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APPENDICES

Appendix 1 References for the climate and trait data used in this study

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher´s website:

Appendix S1 Further details regarding the National Forest Inventories.

Appendix S2 Further methodological details.

Table S1 Main characteristics of the sampling design from the five National Forest Inventories used in this study.

Table S2 List of species present in the plots of the National Forest Inventories included in the analyses.

Table S3 List of initial set of 27 climatic predictors.

Table S4 Trait data used in the study.

Table S5 Estimated parameters and 2-unit support intervals (in brackets) for the best stand growth and mortality models of four forest types.

Fig. S1 Spatial distribution of the response variables in the National Forest Inventories.

Fig. S2 Spatial distribution of the predictor variables in the National Forest Inventories.

Fig. S3 Box-whisker plots of tree growth, tree mortality and sapling abundance along explanatory variables.

Fig. S4 Mean value of the functional traits depending on leaf characteristics used to define forest types.

Fig. S5 Histograms of tree growth, tree mortality and sapling abundance.

Table 1. Mean and 99% percentiles [min., max.] of tree growth (growth, $cm^2\ ha^{-1}\ yr^{-1}$), tree mortality (mortality, $cm^2\ ha^{-1}\ yr^{-1}$), sapling abundance (No. saplings ha^{-1}), stand tree density (No. trees ha^{-1}), mean d.b.h. (mm), potential evapotranspiration (mm), absolute temperature anomaly (ºC), functional diversity (adimensional), and functional identity based on leaf mass per area ($g\ m^{-2}$) for each forest type. Number of plots and main species composition of each forest type (and percentage represented) is also given.

	Broad-leaved deciduous	Mediterranean broad-leaved evergreen	Mediterranean needle-leaved evergreen	Other needle-leaved evergreen
Growth ($cm^2\ ha^{-1}\ yr^{-1}$)	40.99 [0.73, 172.41]	13.63 [0.3, 129.95]	36.04 [1.07, 154.17]	51.43 [0.53, 228.62]
Mortality (% zeros) ($cm^2\ ha^{-1}\ yr^{-1}$)	7.86 (79.11%) [0, 153.82]	3.81 (86.58%) [0, 117.19]	16.97 (68.29%) [0, 245.32]	8.22 (80.82%) [0, 175.05]
Sapling abundance (% zeros) (No. saplings ha^{-1})	1509 (44.31%) [0, 21759]	1169 (31.03%) [0, 6629]	1018 (25.09%) [0, 6366]	1204 (48.59%) [0, 13512]
Density (No. trees ha^{-1})	393 [5, 2117]	184 [5, 1394]	310 [9, 1689]	487 [14, 2275]
Mean d.b.h. (mm)	282.5 [103, 902]	303.19 [102, 828]	238.73 [108, 547]	222.71 [103, 589]
Potential evapotranspiration (mm)	810 [438, 1229]	1107 [781, 1349]	1050 [771, 1310]	739 [432, 1134]
Temperature anomaly (ºC)	0.4 [-0.07, 0.92]	0.53 [0.25, 0.87]	0.54 [0.28, 0.88]	0.44 [-0.25, 1]
Functional diversity	0.06 [0, 0.2]	0.03 [0, 0.25]	0.02 [0, 0.2]	0.04 [0, 0.2]
Functional identity leaf mass per area ($g\ m^{-2}$)	84 [47, 185]	152 [107, 234]	286 [182, 412]	196 [84, 268]
No. plots (% represented)	10,553 (19.42 %)	9,490 (17.50 %)	11,057 (20.39 %)	21,080 (38.88 %)
Composition (% represented)	*Fagus sylvatica, Quercus robur, Q. pyrenaica, Q. petraea, Castanea sativa, Q. faginea,* (70%)	*Quercus ilex, Q. suber* (89.8%)	*Pinus halepensis, P. pinea, P. pinaster* (95%)	*P. sylvestris, Pinus nigra, Picea abies* (81%)

Table 2. Comparisons of alternative models of tree growth (cm^2 ha^{-1} yr^{-1}), tree mortality (cm^2 ha^{-1} yr^{-1}) and sapling abundance (No. saplings ha^{-1}) for the forest types studied using Akaike Information Criterion (AIC).

	ΔAIC													
		Climate effect		Structural effect		Functional composition effect								
Response variable and forest type	Full*	No PET	No TA	No STD	No d_m	No FD	No FI_{LMA}	β_{PET}	β_{TA}	β_{STD}	R^2	Slope	NP
Tree growth													
Broad-leaved deciduous	0	**676**	**220**	**2393**	**130**	**3**	0	**Y**	N	N	0.43	1.00	12
Mediterranean broad-leaved evergreen	0	**329**	**84**	**2549**	**82**	**811**	**3**	N	N	**Y**	0.53	1.00	14
Mediterranean needle-leaved evergreen	0	**182**	**3**	**4568**	**77**	**10**	**1566**	N	N	**Y**	0.54	1.00	14
Other needle-leaved evergreen	20	**3772**	**134**	**6769**	**57**	0	**19**	N	N	N	0.48	1.00	11
Tree mortality													
Broad-leaved deciduous	1	**36**	**18**	**183**	**110**	0	**25**	**Y**	N	N	0.11	1.00	13
Mediterranean broad-leaved evergreen	0	**31**	**5**	**107**	**53**	1	**13**	N	N	N	0.34	1.00	12
Mediterranean needle-leaved evergreen	5	**5**	**21**	**871**	**374**	0	**42**	N	**Y**	**Y**	0.31	1.00	14
Other needle-leaved evergreen	0	**215**	**32**	**348**	**177**	0	**57**	N	**Y**	N	0.22	1.00	14
Sapling abundance													
Broad-leaved deciduous	0	**48**	**26**	**4**	0	**4**	**55**	N	N	N	0.13	1.01	11
Mediterranean broad-leaved evergreen	3	**183**	0	**8**	**121**	**5**	**5**	N	N	N	0.25	1.00	11
Mediterranean needle-leaved evergreen	0	**145**	**22**	0	**9**	**30**	**30**	N	N	N	0.09	1.02	13
Other needle-leaved evergreen	0	**289**	**19**	**79**	**3**	**77**	**36**	**Y**	**Y**	N	0.14	1.01	15

The full models include the effects of potential evapotranspiration (PET, mm), temperature anomaly (TA, ºC), stand tree density (STD, No. trees ha^{-1}), mean d.b.h. (d_m, mm), functional diversity (FD, adimensional) and functional identity based on leaf mass per area (FI_{LMA}, g m^{-2}). The models 'No' ignore the effect of the explanatory variable related. The final predictor variables included in each model are given in bold based on AIC comparison for tree growth, tree mortality and sapling abundance set of models. AIC comparisons (ΔAIC_i) are shown for each set of models

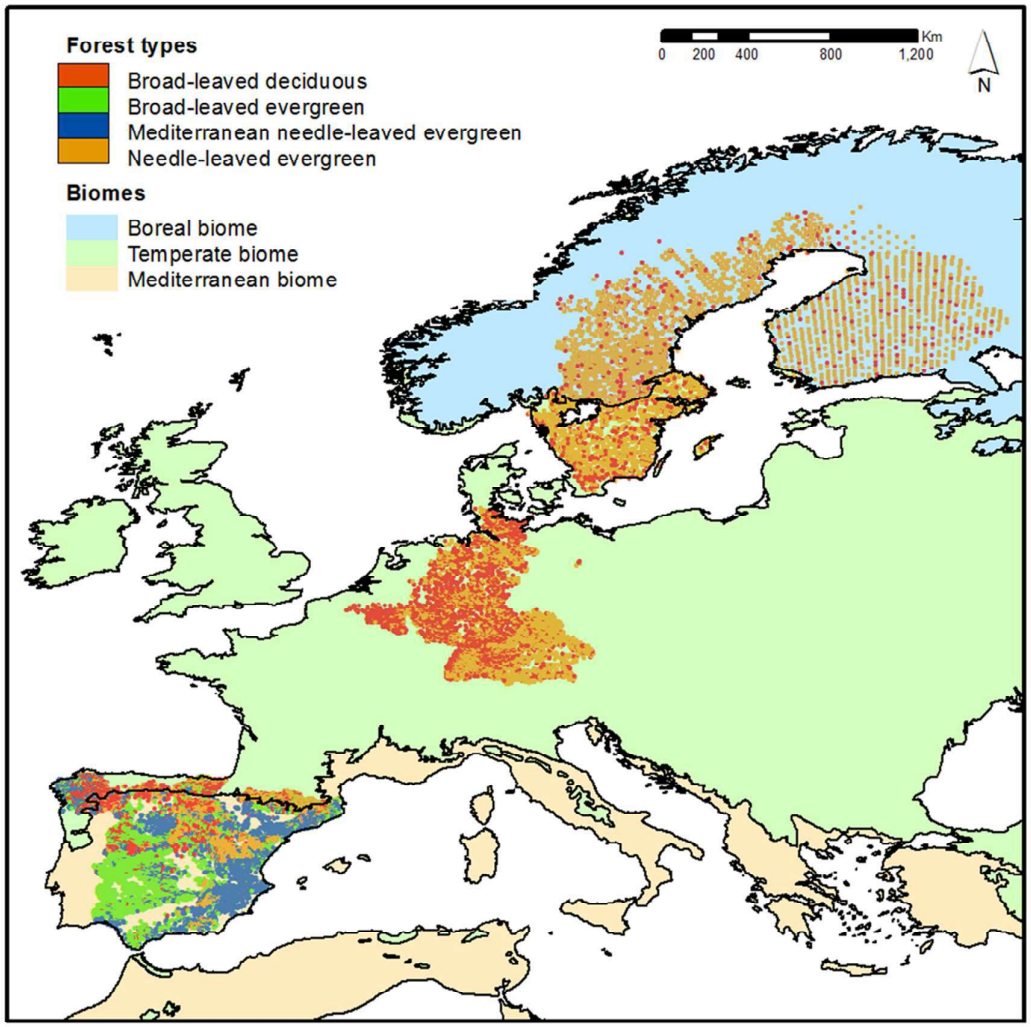
(i.e. tree growth, tree mortality or sapling abundance) through AIC differences of each model (AIC_i) with the model with minimum AIC (AIC_{min}): $\Delta AIC_i = AIC_i - AIC_{min}$. The best model is the one with $\Delta AIC_i = AIC_{min} = 0$. The β columns indicate whether (Y, yes; N, no) the best model included a term that allows evapotranspiration (β_{PET}), temperature anomaly (β_{TA}) or stand tree density (β_{STD}) to vary with functional diversity, changing the breath of the function (see Eqn. (6)). NP is the number of parameters of the final model. The slope and R^2 (1 – SEE/SST) for the relationship between predicted and observed tree growth, tree mortality and sapling abundance are also given.

FIGURE LEGENDS

Figure 1 Spatial distribution of the National Forest Inventory plots for the forest types used in this study and the underlying biome distribution (modified from Olson *et al.*, 2001).

Figure 2 Predicted potential tree growth ($cm^2\ ha^{-1}\ yr^{-1}$), tree mortality ($cm^2\ ha^{-1}\ yr^{-1}$), and sapling abundance (No. saplings ha^{-1}) by functional diversity (adimensional; a, and b for growth and sapling abundance, respectively); and functional identity based on leaf mass per area ($g\ m^2$; c, d, and e, respectively) for each forest type. The forest types include broad-leaved deciduous, Mediterranean broad-leaved evergreen, Mediterranean needle-leaved evergreen, and other needle-leaved evergreen forests. 95% confidence intervals are represented in grey. The predicted potential responses were computed between the minimum and maximum value of the explanatory variable of interest observed in each forest type (see parameter values in Table S5) and the scalars containing the rest of explanatory variables fixed at 1 (see Eqn. (1)).

Figure 3 Predicted potential tree growth ($cm^2\ ha^{-1}\ yr^{-1}$), tree mortality ($cm^2\ ha^{-1}\ yr^{-1}$), and sapling abundance (No. saplings ha^{-1}) by (a) potential evapotranspiration (mm), (b) temperature anomalies (ºC), and (c) stand tree density (No. trees ha^{-1}) for each forest type at two combinations of functional diversity: monospecific forests (i.e. FD = 0) and diverse forests (i.e. FD = 0.2). Dashed lines indicates that the indirect effects of functional diversity determining demographic responses to environment were supported the best model. Confidence intervals are shown in grey. The predicted potential responses were computed between the minimum and maximum value of the explanatory variable of interest observed in each forest type (see parameter values in Table S5) and the scalars containing the rest of explanatory variables fixed at 1 (see Eqn. (1)).



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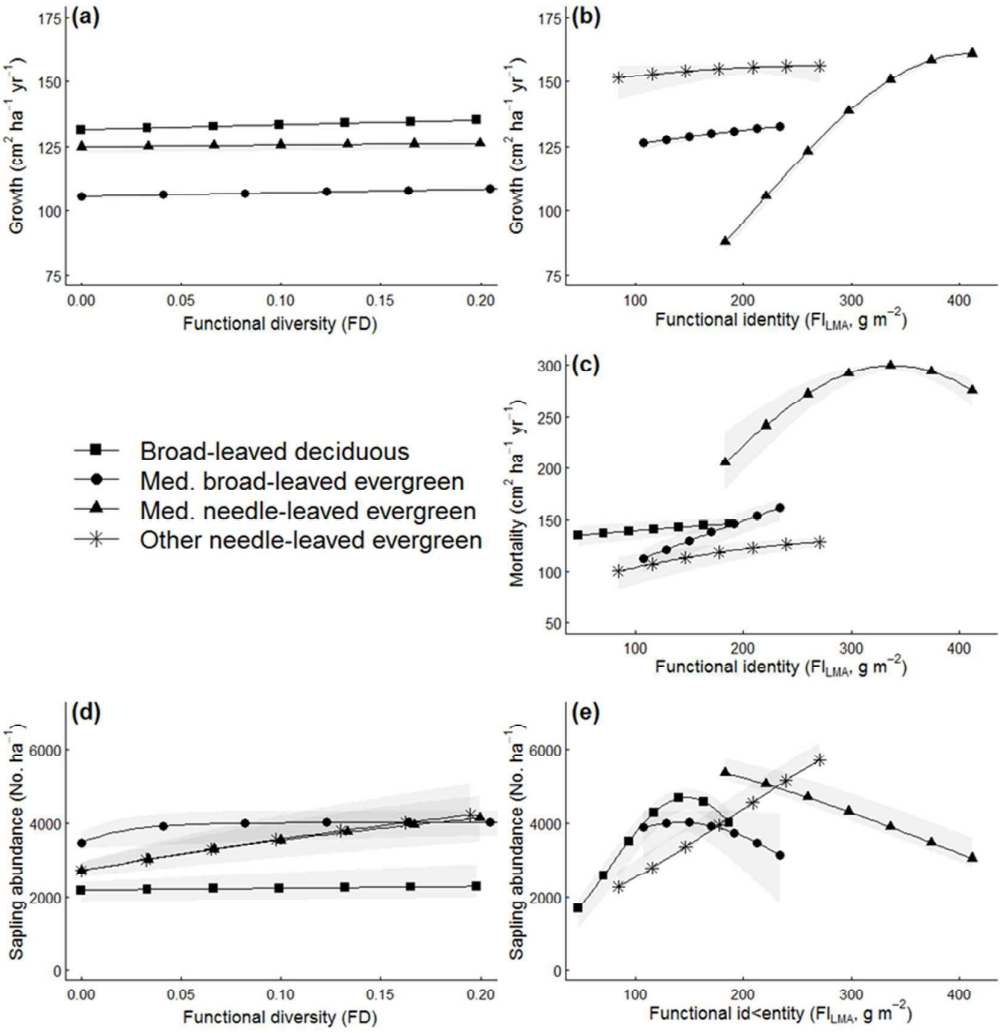
1076 **Figure 1.**



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1078 **Figure 2.**

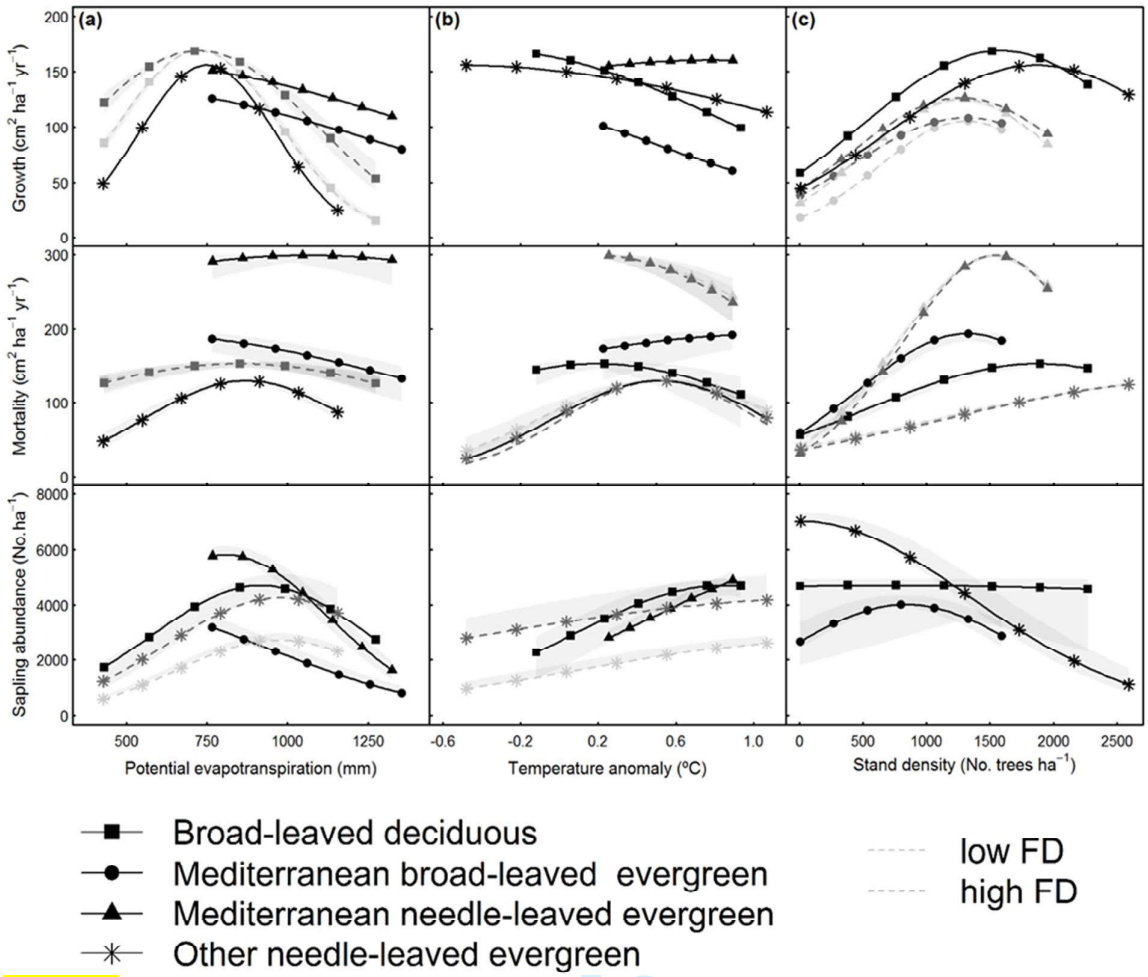

Figure 3.

Supporting Information

Appendix S1 Further details regarding the National Forest Inventories used.

Appendix S2 Further methodological details.

Table S1 Main characteristics of the sampling design from the five National Forest Inventories used in this study.

Table S2 List of species present in the plots of the National Forest Inventories included in the analyses.

Table S3 List of initial set of 27 climatic predictors.

Table S4 Trait data used in the study.

Table S5 Estimated parameters and 2-unit support intervals (in brackets) for the best tree growth, tree mortality models and recruitment models.

Fig. S1 Spatial distribution of the response variables in the National Forest Inventories.

Fig. S2 Spatial distribution of the predictor variables in the National Forest Inventories.

Fig. S3 Box-whisker plots of tree growth, tree mortality and sapling abundance along explanatory variables.

Fig. S4 Mean value of the functional traits depending on leaf characteristics used to define forest types.

Fig. S5 Histograms of tree growth, tree mortality and sapling abundance.

Appendix S1. Further details regarding the National Forest Inventories used

Spanish National Forest Inventory: We used information from the second and third Spanish NFI (surveyed in the periods 1986-1996 and 1997-2007, respectively). The Spanish NFI plots are located on a 1 km^2 grid over forested regions (Villaescusa & Díaz, 1998; Villanueva, 2004). Spanish NFI plots were sampled using a variable radius technique with four concentric circular subplots of radius 5, 10, 15 and 25 m. Within each subplot, trees were included in the sample according to their diameter at breast height (d.b.h.), with trees smaller than 12.4 cm measured in the 5 m radius subplot, those of 12.5-22.4 cm in the 10 m radius subplot, those of 22.5-42.4 cm in the 15 m radius subplot, and those with d.b.h. larger or equal to 42.5 cm in the 25 m radius subplot.

German National Forest Inventory: We used information from the first and second German NFI. The German NFI uses a systematic grid of clusters, sampled in the periods 1986-1990 (undertaken in West Germany only) and 2001-2002 respectively. The size of the sample grid is 4 by 4 km, however, it is reduced in some federal states to either 2.83 by 2.83 km or 2 by 2 km. Each cluster is a quadrangle of 150 m in length with a sample plot on each corner (Kändler, 2009). Trees with a d.b.h. of 10 cm or more in the first inventory and 7 cm in the second were selected by the angle-count method with a basal area factor (BAF) of 4 $m^2 ha^{-1}$ if they are alive or recently dead.

Walloon National Forest Inventory (Belgium): The Walloon NFI follows a systematic non-stratified sampling methodology on a 1 km by 0.5 km grid. One circular sampling plot is located within each grid intersection. Areas are sampled if the area of land is greater than 0.1 ha and has at least 10% covered by a forest canopy (trees must be able to reach a minimum of

5 m). Plots in the first census were surveyed between 1994 and 2003 and plots in the second census were surveyed between 2008 and 2011. The inventory employs a variable plot size depending on the circumference of the tree: trees from 70 to 119 mm in 9 m radius; and greater than 120 cm in 18 m radius.

Swedish National Forest Inventory: The permanent inventory uses a randomly planned regular sampling grid and includes about 4,500 permanent tracts, each surveyed every five years. Plots in the first census were surveyed between 2003 and 2005 and plots in the second census were surveyed between 2008 and 2010. The tracts are rectangular and have different dimensions depending on the location within the country. Each tract has between 4 and 8 circular sample plots. Trees greater than 10 cm d.b.h. are sampled in a 10 m radius.

Finnish National Forest Inventory: We used information from the two consecutives surves of NFI8 sampled in the period 1985-1986 to 1995. The sample plots are in a systematic grid across the country of plot clusters in forested areas (Mäkipää & Heikkinen, 2003). In Southern Finland the grid is 16 by 16 square km, with four plots in each cluster at 400 m. intervals, while in Northern Finland the grid is a 24 by 32 km rectangle with three plots per cluster, at 600 m. intervals. These permanent sample plot data were sampled using a variable radius technique with two concentric circular subplots of radius 5.64 m for trees under 10.5 cm of d.b.h. (i.e. 100 m^2) and 9.77 m for trees of d.b.h. 10.5 cm or higher (i.e. 300 m^2).

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Appendix S2. Further methodological details

Plot selection and response variables:

From the initial plots of the five NFI we selected a total 54,224 plots resulting from different criteria: (i) at least one adult tree was measured with a minimum d.b.h. of 10 cm or more in consecutive surveys (i.e. d.b.h. > 10 cm), (ii) there was no evidence of thinning or harvesting in the second NFI, and (iii) plots had growth and mortality of less than the 99.99% upper quartile to remove outliers.

As response variables we used absolute tree growth, tree mortality and sapling abundance. We selected absolute tree growth and mortality (cm^2 ha^{-1} yr^{-1}) instead of relative growth and mortality rates (%) because: (i) demographic variables in absolute terms are widely used in studies investigating the effect of diversity and complementarity effects (e.g. Paquette & Messier, 2011; Laksy *et al.*, 2014); (ii) they allow a direct comparison of the changes on tree growth and mortality, which is of interest across ecosystem development (Odum, 1969); and (iii) absolute demographic rates are better proxies of changes in biomass than relative demographic rates, although absolute demographic rates might be affected by initial stand basal area (e.g. Sheil, 1995; Vayreda *et al.*, 2012; Ruiz-Benito *et al.*, 2015).

Trait-based indices calculation:

143 species were present in the 54,224 plots selected for this study (122 at species level and 21 at genus level; see Table S2). To calculate trait-based diversity indices we used four functional traits that have been shown to greatly influence tree performance: maximum tree height (MTH, m), wood density (WD, g cm^{-3}), seed mass (SM, mg) and leaf mass per area (LMA, g m^{-2}) (e.g. Paquette & Messier, 2011; Swenson *et al.*, 2012; Ruiz-Benito *et al.*, 2014). Trait weights and NA (no available data) were carefully considered in the calculations. When NAs are few, especially for rare species, the benefits of keeping that trait are higher

than the drawbacks. To avoid potential negative effects of missing data, we checked that the missing values were less than 15% of species documented for each trait.

We computed functional diversity using functional dispersion (FD; Laliberté & Legendre, 2010) and functional identity (FI) using community-weighted means of trait values (Lavorel *et al.* 2008). From the large dataset of 54,224 plots from the five NFI selected, we computed the stand basal area (m^2 ha^{-1}) of each species present in each plot. This was used as a matrix of species abundance and presence–absence of species to functional diversity (FD) and functional identity (FI). These analyses were performed using R 3.2. (R Core Team, 2015) and the FD package (Laliberté & Legendre, 2010).

Functional dispersion (FD) is a multidimensional index of functional diversity and using presence-absence matrices FD is the mean distance in a multidimensional trait space of individual species to the centroid (center of mass) of all species present in a certain plot. Thus, FD was calculated using the next equation (Laliberte and Legendre, 2010):

$$FD = \frac{\sum_{j=1}^{j=n} z_j}{n}$$

Where n is the number of individual species z_j is the distance of the species j to the centroid c. The centroid c for one trait i is just the mean value of that trait for the j species present in the plot (i.e. from 1 to n species). For example, FD for a monospecific plot would have a value of zero, increasing as the dispersion of the traits selected increase in the plot.

Functional identity was measured through community-weighted means, as a direct extension of the "mass ratio hypothesis" and relates to functional composition (Grime, 1998). Community-weighted means is defined as the mean values of traits of species present in the community weighted by the relative abundance of taxa. Community-weighted means (CWM) was calculated as (Lavorel *et al.* 2008):

$$\text{CWM} = \sum_{i=1}^{n} p_i \times trait_i$$

Where p_i is the relative contribution of species i to the community, and $trait_i$ is the trait value of species i.

Predictors of demographic responses:

The final potential drivers of tree growth, tree mortality and sapling abundance patterns selected were stand tree density, mean d.b.h., potential evapotranspiration, absolute temperature anomaly, functional diversity and functional identity (see Figs. S3-S4). We calculated the variance inflation factor (VIF) and correlation between the each predictor variable using usdm package (Babak, 2015) in R 3.2 (R Core Team, 2015) and our results confirm that collinearity was not a major problem for the models calculated (VIF < 2, r < 0.4; Dormann *et al.*, 2013).

Correction for sampling heterogeneity:

The census intervals in our dataset varied between 5 and 16 years (mean = 10.7 years, sd = 2.8 years). We tested the influence of census interval through a modification of parameter μ_{pot}, which represents the maximum demographic response (i.e. maximum value of tree growth, tree mortality or sapling abundance when the all potential predictors are at their optimal values) (see Eqn. (1)) in the main manuscript. We compared the best models of tree growth, tree mortality and sapling abundance with the same models where the parameter μ_{pot} varied depending on census interval following the functional form:

$$\mu_{pot} = \mu'_{pot} - \alpha_0 \times census\ interval \qquad \text{Eqn (S1.1)}$$

where *census interval* is the number of years between surveys and μ'_{pot} and α_0 are parameters estimated by our model. Parameter estimation, model comparison and model selection was performed using the same methods than the main manuscript. We did not find support for a

modification of the parameter μ_{pot} depending on census interval, and, therefore, a modified parameter was not included in the final best model (Table S2.1). Additionally, we also checked the residuals of the best model against census interval and we did not find any pattern (Figure S2.1).

Considering the influence of plot size on the demographic rates, it was not possible to follow the same approach because not all the NFIs used a fixed radius for each plot (i.e. a certain tree was measured depending on its size of and the position to the centre of the plot, see Table S1 and Appendix S1). Two of the four forest types present in our study area were only located in Spain, and, therefore, sampling methods were constant along the entre forest (i.e. Mediterranean needle-leaved and broad-leaved evergreen). To be sure that NFI sampling methods were not affecting our results and conclusions we modelled the residuals of each demographic response for those forest types present in more than one NFI (i.e. broad-leaved deciduous and needle-leaved evergreen forests) and we did not find any clear patterns (see Fig. S2.2).

Table S2.1 Comparison of alternative models for each forest type and demographic response, including the influence of census interval (No. years) on demographic responses (i.e. modification of demographic response folowing Eqn. (S1), AIC_{CI}) or without the additional parameter (AIC_{best}). $\Delta AIC_{(CI\text{-}best)}$ is the difference in AIC units between the two models. The inclusion of an additional parameter to account for the influence of census interval was not supported in any of the models.

	AIC_{CI}	AIC_{best}	$\Delta AIC_{(CI\text{-}best)}$
Tree growth			
Broad-leaved deciduous	97964	95265	**2698.54**
Med. broad-leaved evergreen	69187	68862	**325.71**
Med. needle-leaved evergreen	96837	96182	**654.98**
Other needle-leaved evergreen	211665	203328	**8337.30**
Tree mortality			
Broad-leaved deciduous	20761	20663	**98.71**
Med. broad-leaved evergreen	11491	11455	**36.17**
Med. needle-leaved evergreen	36009	35599	**410.03**
Other needle-leaved evergreen	39840	39346	**493.78**
Sapling abundance			
Broad-leaved deciduous	124402	124330	**71.60**
Med. broad-leaved evergreen	127981	127980	**0.70**
Med. needle-leaved evergreen	154094	153985	**108.40**

Other needle-leaved evergreen	231030	231031	**-0.50**

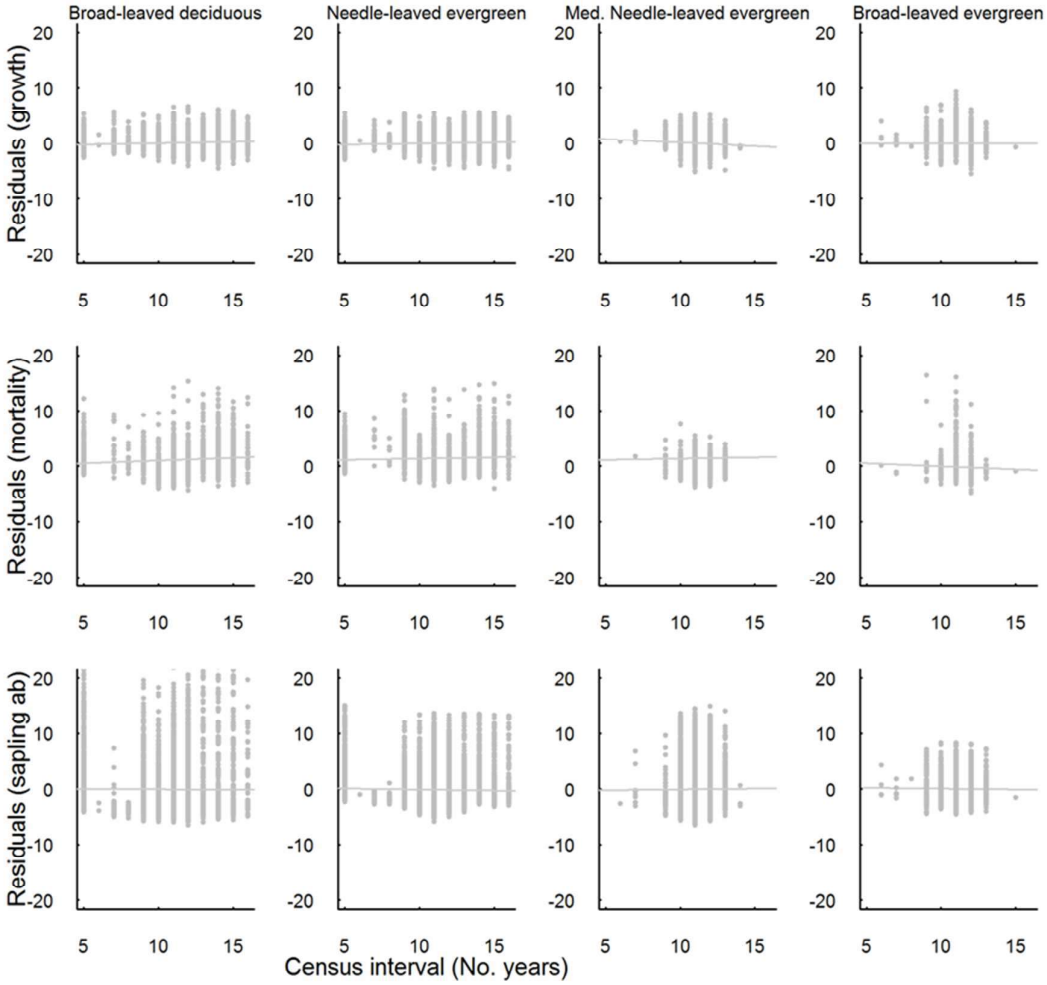

Figure S2.1. Scatterplot of residuals of the best models selected for each forest type for tree growth, tree mortality and sapling abundance against census interval. A linear regression line between the residuals and the census interval is shown.

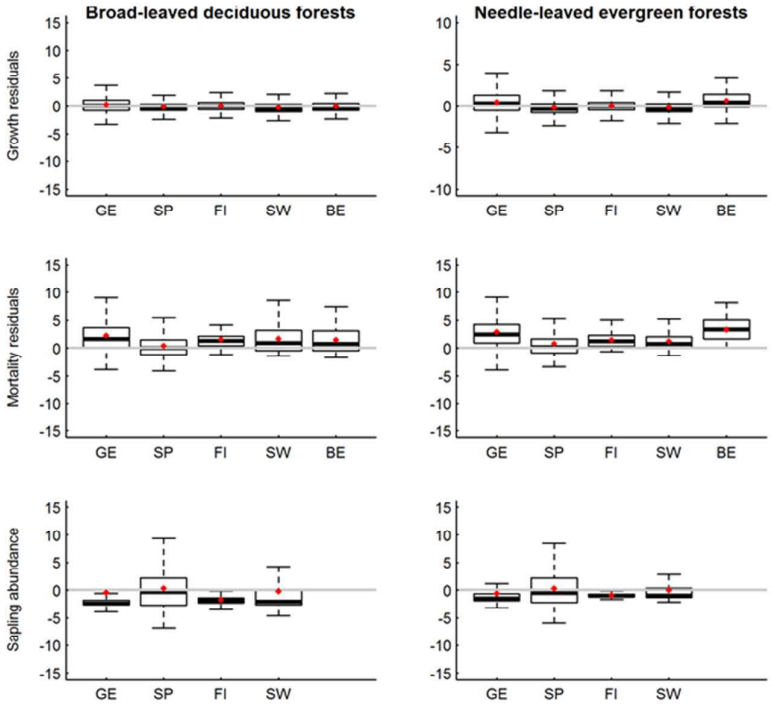

Figure S2.2. Boxplot of residuals of the selected models of tree growth, tree mortality and sapling abundance for each NFI for broad-leaved deciduous and needle-leaved evergreen forests (i.e. forests covering more than one country across Europe). Wallonia is not shown for residuals of sapling abundance models because the sapling abundance data was not available. Mean values for each country are show in red. Tukey´s post-hoc comparison of country means are included.

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Table S1. Main characteristics of the plot and sampling design of the National Forest Inventories

	Spain	Germany	Wallonia (Belgium)	Sweden	Finland
Survey dates	1986/96, 1997/2007	1986/90, 2001/02	1994/2003, 2008/11	2005/10, 2008/10	1985/86, 1995
Mean (No. years) [98th percentiles]	11.15 [9,13]	14.30 [12,16]	9.86 [7, 15]	5 [5,5]	9.15 [9,10]
Sample plot design	Single sample plots 1 by 1 km grid	Cluster design 4 by 4 km grid (vary) 4 plots in a cluster	Single sample plots 1 by 0.5 km grid	Cluster design Vary	Cluster design 16 by 16 km grid (vary) 10, 11, 14 plots in a cluster.
Sample tree survey design	Variable radius	Angle-count	Variable radius	Variable radius	Variable radius
Plot size (m^2)	79, 315, 707, 1964	BAF = 4 m^2 ha^{-1}	63, 254, 1017	38, 314	100, 300
Minimum adult tree d.b.h. (cm)	7.5	10, 7	6.4	4	1
Sapling abundance (plot size, m^2)	0.3 m < height < 1.3 m (79)	0.3 m < height < 1.3 m (9.6)	No data	0.3 m < height < 1.3 m (38)	0.3 m < height < 1.3 m (100)

Table S2. List of species names, genus and family and forest type.
We followed the nomenclature of *Atlas Florae Europaea*. The forest types are based on the leaf type (i.e. BL: broad-leaved, NL: needle-leaved, DEC: deciduous, EVE: evergreen) and Mediterranean character (i.e. med).

Name	Genus	Family	Forest type
Abies alba Mill.	*Abies*	*Pinaceae*	NL-EVE
Abies grandis (D.Don) Lindl.	*Abies*	*Pinaceae*	NL-EVE
Abies pinsapo Boiss.	*Abies*	*Pinaceae*	NL-EVE
Abies procera Rehder	*Abies*	*Pinaceae*	NL-EVE
Abies spp.	*Abies*	*Pinaceae*	NL-EVE
Acacia dealbata Link	*Acacia*	*Leguminosae*	BL-EVE
Acacia melanoxylon R.Br.	*Acacia*	*Leguminosae*	BL-EVE
Acacia spp.	*Acacia*	*Leguminosae*	BL-EVE
Acer campestre L.	*Acer*	*Aceraceae*	BL-DEC
Acer monspessulanum L.	*Acer*	*Aceraceae*	BL-DEC
Acer negundo L.	*Acer*	*Aceraceae*	BL-DEC
Acer opalus Mill.	*Acer*	*Aceraceae*	BL-DEC
Acer platanoides L.	*Acer*	*Aceraceae*	BL-DEC
Acer pseudoplatanus L.	*Acer*	*Aceraceae*	BL-DEC
Aesculus hippocastanum L.	*Aesculus*	*Hippocastanaceae*	BL-DEC
Alnus glutinosa (L.) Gaertn.	*Alnus*	*Betulaceae*	BL-DEC
Alnus incana (L.) Moench	*Alnus*	*Betulaceae*	BL-DEC
Alnus spp.	*Alnus*	*Betulaceae*	BL-DEC
Alnus viridis (Chaix) DC.	*Alnus*	*Betulaceae*	BL-DEC
Arbutus canariensis Veill.	*Arbutus*	*Ericaceae*	BL-EVE
Arbutus unedo L.	*Arbutus*	*Ericaceae*	BL-EVE
Betula pendula Roth	*Betula*	*Betulaceae*	BL-DEC
Betula pubescens Ehrh.	*Betula*	*Betulaceae*	BL-DEC
Betula spp.	*Betula*	*Betulaceae*	BL-DEC
Carpinus betulus L.	*Carpinus*	*Betulaceae*	BL-DEC
Castanea sativa Mill.	*Castanea*	*Fagaceae*	BL-DEC
Cedrus atlantica (Endl.) Carrière	*Cedrus*	*Pinaceae*	NL-EVE
Cedrus deodara (D.Don) G.Don	*Cedrus*	*Pinaceae*	NL-EVE
Cedrus libani A.Rich.	*Cedrus*	*Pinaceae*	NL-EVE
Celtis australis L.	*Celtis*	*Ulmaceae*	BL-DEC
Ceratonia siliqua L.	*Ceratonia*	*Leguminosae*	BL-EVE
Chamaecyparis lawsoniana (A.Murray bis) Parl.	*Chamaecyparis*	*Cupressaceae*	NL-EVE
Corylus avellana L.	*Corylus*	*Betulaceae*	BL-DEC
Crataegus monogyna Jacq.	*Crataegus*	*Rosaceae*	BL-DEC
Crataegus spp.	*Crataegus*	*Rosaceae*	BL-DEC
Cupressus arizonica Greene	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus lusitanica Mill.	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus macrocarpa Hartw.	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus sempervirens L.	*Cupressus*	*Cupressaceae*	NL-EVE
Erica arborea L.	*Erica*	*Ericaceae*	NL-EVE
Eucalyptus camaldulensis Dehnh.	*Eucalyptus*	*Myrtaceae*	BL-EVE

Name	Genus	Family	Forest type
Eucalyptus globulus Labill.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus gomphocephalus DC.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus nitens (H.Deane & Maiden) Maiden	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus viminalis Labill.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Fagus sylvatica L.	*Fagus*	*Fagaceae*	BL-DEC
Ficus carica L.	*Ficus*	*Moraceae*	BL-DEC
Frangula alnus Mill.	*Frangula*	*Rhamnaceae*	BL-DEC
Fraxinus americana L.	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus angustifolia Vahl	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus excelsior L.	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus ornus L.	*Fraxinus*	*Oleaceae*	BL-DEC
Ilex aquifolium L.	*Ilex*	*Aquifoliaceae*	BL-EVE
Ilex canariensis Poir.	*Ilex*	*Aquifoliaceae*	BL-EVE
Juglans regia L.	*Juglans*	*Juglandaceae*	BL-DEC
Juniperus communis L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus oxycedrus L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus phoenicea L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus spp.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus thurifera L.	*Juniperus*	*Cupressaceae*	NL-EVE
Larix decidua Mill.	*Larix*	*Pinaceae*	NL-EVE
Larix kaempferi (Lamb.) Carrière sec. Franco	*Larix*	*Pinaceae*	NL-DEC
Larix spp.	*Larix*	*Pinaceae*	NL-EVE
Laurus azorica (Seub.) Franco	*Laurus*	*Lauraceae*	NL-EVE
Laurus nobilis L.	*Laurus*	*Lauraceae*	BL-EVE
Malus sylvestris Mill.	*Malus*	*Rosaceae*	BL-DEC
Morus spp.	*Morus*	*Moraceae*	BL-DEC
Myrica faya Aiton	*Myrica*	*Myricaceae*	BL-EVE
Olea europaea L.	*Olea*	*Oleaceae*	BL-EVE
Persea indica (L.) Spreng.	*Persea*	*Lauraceae*	BL-EVE
Phillyrea latifolia L.	*Phillyrea*	*Oleaceae*	BL-EVE
Phoenix spp.	*Phoenix*	*Arecaceae*	BL-EVE
Picconia excelsa (Aiton) DC.	*Picconia*	*Oleaceae*	BL-EVE
Picea abies (L.) H.Karst.	*Picea*	*Pinaceae*	NL-EVE
Picea omorika (PancKicA) Purk.	*Picea*	*Pinaceae*	NL-EVE
Picea pungens Engelm.	*Picea*	*Pinaceae*	NL-EVE
Picea sitchensis (Bong.) Carrière	*Picea*	*Pinaceae*	NL-EVE
Picea spp.	*Picea*	*Pinaceae*	NL-EVE
Pinus canariensis Sweet ex Spreng.	*Pinus*	*Pinaceae*	NL-EVE
Pinus contorta Douglas ex Loudon	*Pinus*	*Pinaceae*	NL-EVE
Pinus halepensis Mill.	*Pinus*	*Pinaceae*	$NL\text{-}EVE_{med}$
Pinus mugo Turra	*Pinus*	*Pinaceae*	NL-EVE
Pinus nigra J.F.Arnold	*Pinus*	*Pinaceae*	NL-EVE
Pinus pinaster Aiton	*Pinus*	*Pinaceae*	$NL\text{-}EVE_{med}$
Pinus pinea L.	*Pinus*	*Pinaceae*	$NL\text{-}EVE_{med}$

Name	Genus	Family	Forest type
Pinus ponderosa Douglas ex P.Lawson & C.Lawson	*Pinus*	*Pinaceae*	NL-EVE
Pinus radiata D.Don	*Pinus*	*Pinaceae*	NL-EVE
Pinus spp.	*Pinus*	*Pinaceae*	NL-EVE
Pinus strobus L.	*Pinus*	*Pinaceae*	NL-EVE
Pinus sylvestris L.	*Pinus*	*Pinaceae*	NL-EVE
Pinus uncinata Mill. ex Mirb.	*Pinus*	*Pinaceae*	NL-EVE
Pistacia terebinthus L.	*Pistacia*	*Anacardiaceae*	BL-DEC
Platanus hispanica Ten.	*Platanus*	*Platanaceae*	BL-DEC
Populus alba L.	*Populus*	*Salicaceae*	BL-DEC
Populus balsamifera Brayshaw	*Populus*	*Salicaceae*	BL-DEC
Populus nigra L.	*Populus*	*Salicaceae*	BL-DEC
Populus spp.	*Populus*	*Salicaceae*	BL-DEC
Populus tremula L.	*Populus*	*Salicaceae*	BL-DEC
Populus x canadensis Moench	*Populus*	*Salicaceae*	BL-DEC
Prunus avium L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus lusitanica L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus padus L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus serotina Ehrh.	*Prunus*	*Rosaceae*	BL-DEC
Prunus spinosa L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus spp.	*Prunus*	*Rosaceae*	BL-DEC
Pseudotsuga menziesii (Mirb.) Franco	*Pseudotsuga*	*Pinaceae*	NL-EVE
Pyrus spp.	*Pyrus*	*Rosaceae*	BL-DEC
Quercus canariensis Willd.	*Quercus*	*Fagaceae*	BL-DEC
Quercus faginea Lam.	*Quercus*	*Fagaceae*	BL-DEC
Quercus ilex L.	*Quercus*	*Fagaceae*	BL-EVE
Quercus palustris Münchh.	*Quercus*	*Fagaceae*	BL-DEC
Quercus petraea (Matt.) Liebl.	*Quercus*	*Fagaceae*	BL-DEC
Quercus pubescens Willd. (Q. Humilis)	*Quercus*	*Fagaceae*	BL-DEC
Quercus pyrenaica Willd.	*Quercus*	*Fagaceae*	BL-DEC
Quercus robur L.	*Quercus*	*Fagaceae*	BL-DEC
Quercus rubra L.	*Quercus*	*Fagaceae*	BL-DEC
Quercus spp.	*Quercus*	*Fagaceae*	BL-DEC
Quercus suber L.	*Quercus*	*Fagaceae*	BL-EVE
Rhamnus alaternus L.	*Rhamnus*	*Rhamnaceae*	BL-EVE
Robinia pseudacacia L.	*Robinia*	*Leguminosae*	BL-DEC
Salix alba L.	*Salix*	*Salicaceae*	BL-DEC
Salix atrocinerea Brot.	*Salix*	*Salicaceae*	BL-DEC
Salix caprea L.	*Salix*	*Salicaceae*	BL-DEC
Salix elaeagnos Scop.	*Salix*	*Salicaceae*	BL-DEC
Salix fragilis L.	*Salix*	*Salicaceae*	BL-DEC
Salix spp.	*Salix*	*Salicaceae*	BL-DEC
Sambucus nigra L.	*Sambucus*	*Caprifoliaceae*	BL-DEC
Sorbus aria (L.) Crantz	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus aucuparia L.	*Sorbus*	*Rosaceae*	BL-DEC

Name	Genus	Family	Forest type
Sorbus domestica L.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus intermedia (Ehrh.) Pers.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus spp.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus torminalis (L.) Crantz	*Sorbus*	*Rosaceae*	BL-DEC
Tamarix spp.	*Tamarix*	*Tamaricaceae*	NL-EVE
Taxus baccata L.	*Taxus*	*Taxaceae*	NL-EVE
Thuja spp.	*Thuja*	*Cupressaceae*	NL-EVE
Tilia cordata Mill.	*Tilia*	*Tiliaceae*	BL-DEC
Tilia platyphyllos Scop.	*Tilia*	*Tiliaceae*	BL-DEC
Tilia spp.	*Tilia*	*Tiliaceae*	BL-DEC
Tsuga spp.	*Tsuga*	*Pinaceae*	NL-EVE
Ulmus glabra Huds.	*Ulmus*	*Ulmaceae*	BL-DEC
Ulmus minor Mill.	*Ulmus*	*Ulmaceae*	BL-DEC
Ulmus spp.	*Ulmus*	*Ulmaceae*	BL-DEC

Table S3. List of initial set of 27 climatic predictors.
We used data from WorldClim (Hijmans *et al.*, 2005), CGIAR-CSI GeoPortal (using CGIAR-CSI Global-Aridity and Global-PET Database (Zomer *et al.,* 2008)), SPEIbase v2.2. (Beguería *et al.*, 2010; Vicente-Serrano *et al.*, 2010) and UDel_AirT_Precip data provided by the NOAA/OAR/ESRL PSD (Boulder, Colorado, USA).

CODE	VARIABLE	UNITS	DEFINITION
MSPEI	Mean standardised precipitation-evapotranspiration index	adimensional	With a value for *PET*, the difference between the precipitation (*P*) and *PET* for the month *i* is calculated: $D_i = PET_i - P_i$, standardised according to a log-logistic distribution. Mean value between the two consecutuves inventories
FDY	Frequency of dry years	No. years	No. of years from 1982 to 2010 with SPEI < 0
ID	Most intense drought	adimensional	Lowest SPEI value from 1982 to 2010
PET	Global potential evapotranspiration	mm	$PET = 0.0023 \times RA \times (Tmean + 17.8) \times TD0.5$, where *Tmean* is monthly temperature, *RA* is extra-terrestrial radiation and *TD* is temperature range.
Aridity	Global potential aridity	adimensional	Quantify precipitation availability over atmospheric water demand using the ratio between mean annual precipitation and PET
WAI	Water availability index	%	Difference between precipitation and evapotranspiration relative to evapotranspiration (%)
BIO1	Annual mean temperature	ºC	The mean of all the weekly mean temperatures
BIO2	Mean diurnal range	ºC	The mean of all the weekly diurnal temperature ranges
BIO3	Isothermality	%	The mean diurnal range divided by the annual temperature range
BIO4	Temperature seasonality	ºC	Standard deviation *100
BIO5	Max temperature of warmest month	ºC	Highest temperature of any weekly maximum temperature.
BIO6	Min temperature of coldest month	ºC	Lowest temperature of any weekly minimum temperature.
BIO7	Temperature annual range	ºC	Difference between BIO5 and BIO6
BIO8	Mean temperature of wettest quarter	ºC	The wettest quarter of the year is determined (to the nearest week), and the mean temperature of this period is calculated.
BIO9	Mean temperature of	ºC	The driest quarter of the year is determined (to the nearest week), and the mean

CODE	VARIABLE	UNITS	DEFINITION
	driest quarter		temperature of this period is calculated.
BIO10	Mean temperature of warmest quarter	ºC	The warmest quarter of the year is determined (to the nearest week), and the mean temperature of this period is calculated.
BIO11	Mean temperature of coldest quarter	ºC	The coldest quarter of the year is determined (to the nearest week), and the mean temperature of this period is calculated.
BIO12	Annual precipitation	mm	The sum of all the monthly precipitation estimates.
BIO13	Precipitation of wettest month	mm	The precipitation of the wettest week or month, depending on the time step.
BIO14	Precipitation of driest month	mm	The precipitation of the driest week or month, depending on the time step.
BIO15	Precipitation seasonality (coefficient of variation)	mm	The coefficient of variation is the standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean).
BIO16	Precipitation of wettest quarter	mm	The wettest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.
BIO17	Precipitation of driest quarter	mm	The driest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.
BIO18	Precipitation of warmest quarter	mm	Warmest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.
BIO19	Precipitation of coldest quarter	mm	The coldest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.
TA	Temperature anomaly	ºC	Difference between the mean temperature for the study period and the mean value for the reference period (1900-2010)
PA	Precipitation anomaly	%	Difference between the annual precipitation for the study period and the mean value for the reference period (1900-2010) respect to the mean value for precipitation for the reference period

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Zomer, R.J., Trabucco, A., Bossio, D.A. & Verchot, L.V. (2008) Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystem & Environment*, **126**, 67-80.

Table S4. Functional traits used to compute trait-based diversity indices. Trait type, transformation (when applicable), number of missing data for the 143 species initially considered (i.e. data not available, No. NA) and the sources and references used are given. See Appendix 1 for a complete list of references.

Trait	Unit	No. NA	Transformation	Sources and references
Maximum tree height	m	0		Tree height was calculated as the 99.99 % percentile of the distribution of tree heights measured for each species from the first National Forest Inventory for the five countries (see Appendix S1).
Wood density	g cm^{-3}	2		(Castro-Díez *et al.* 1998; Cornelissen *et al.* 2003; Ogaya & Peñuelas 2003; Cornwell *et al.* 2006; Ogaya & Peñuelas 2006; Preston *et al.* 2006; Ackerly & Cornwell 2007; Ogaya & Peñuelas 2007; Kleyer *et al.* 2008; Ogaya & Peñuelas 2008; Sardans *et al.* 2008a; Sardans *et al.* 2008b; Chave *et al.* 2009; Cornwell & Ackerly 2009; Reich *et al.* 2009; Zanne *et al.* 2009; Ordonez *et al.* 2010a; Ordonez *et al.* 2010b)
Seed mass	mg	4	Natural log	(Cornelissen 1996; Otto 2002; Díaz *et al.* 2004; Kühn *et al.* 2004; Moles *et al.* 2004; Sack 2004; Moles *et al.* 2005a; Moles *et al.* 2005b; Cornwell *et al.* 2006; Preston *et al.* 2006; Ackerly & Cornwell 2007; Garnier *et al.* 2007; Kew 2008; Kleyer *et al.* 2008; Pakeman *et al.* 2008; Paula & Pausas 2008; Quero *et al.* 2008a; Cornwell & Ackerly 2009; Fortunel *et al.* 2009; Green 2009; Pakeman *et al.* 2009; Paula *et al.* 2009; Laughlin *et al.* 2010)
Leaf mass per area	g m^2	1		(Cornelissen 1996; Cornelissen *et al.* 1996; Cornelissen *et al.* 1997; Atkin *et al.* 1999; McKenna & Shipley 1999; Medlyn *et al.* 1999; Medlyn & Jarvis 1999; Meziane & Shipley 1999; Niinemets 1999; Fonseca *et al.* 2000; Medlyn *et al.* 2001; Niinemets 2001; Shipley 2002; Shipley & Vu 2002; Cornelissen *et al.* 2003; Loveys *et al.* 2003; McDonald *et al.* 2003; Ogaya & Peñuelas 2003; Poschlod *et al.* 2003; Quested *et al.* 2003; Sack *et al.* 2003; Cornelissen *et al.* 2004; Díaz *et al.* 2004; Sack 2004; Wright *et al.* 2004; Cavender-Bares *et al.* 2006; Cornwell *et al.* 2006; Ogaya & Peñuelas 2006; Preston *et al.* 2006; Sack *et al.* 2006; Wright *et al.* 2006; Ackerly & Cornwell 2007; Campbell *et al.* 2007; Garnier *et al.* 2007; Ogaya & Peñuelas 2007; Coomes *et al.* 2008; Cornwell *et al.* 2008; Kleyer *et al.* 2008; Ogaya & Peñuelas 2008; Pakeman *et al.* 2008; Quero *et al.* 2008b; Reich & Oleksyn 2008; Sardans *et al.* 2008a; Sardans *et al.* 2008b; Cornwell & Ackerly 2009; Fortunel *et al.* 2009; Kattge *et al.* 2009; Pakeman *et al.* 2009; Poorter *et al.* 2009; Reich *et al.* 2009; Freschet *et al.* 2010b, a; Laughlin *et al.* 2010; Ordonez *et al.* 2010a; Ordonez *et al.* 2010b; Willis *et al.* 2010; Onoda *et al.* 2011)

Table S5. Parameters for the final models of tree growth, tree mortality and sapling abundance.

Mean and 95% confidence intervals of the model parameters of **(A)** tree growth, **(B)** tree mortality, and **(C)** sapling abundance for each of the four forest types defined (Eqns. (1)-(6)).

(A)	Broad-leaved deciduous	Mediterranean broad-leaved evergreen	Mediterranean needle-leaved evergreen	Other needle-leaved evergreen
$XPET_a$	724.44 [724.44, 731.68]	400.00 [400, 408]	400.00 [400, 412]	750.39 [750.39, 750.39]
$XPET_b$	250.95 [243.42, 258.48]	930.10 [902.19, 941.5]	1056.28 [1035.15, 1077.4]	211.85 [209.73, 213.97]
XTA_a	-0.36 [-0.38, -0.33]	-0.80 [-0.8, -0.78]	0.78 [0.62, 0.9]	-0.53 [-0.57, -0.49]
XTA_b	1.25 [1.22, 1.28]	1.33 [1.32, 1.34]	2.00 [1.66, 2]	2.00 [1.94, 2]
$XSTD_a$	1582.74 [1582.74, 1582.74]	1311.45 [1311.45, 1311.45]	1272.77 [1272.77, 1272.77]	1865.91 [1865.91, 1865.91]
$XSTD_b$	1082.97 [1082.97, 1082.97]	693.22 [693.22, 693.22]	766.89 [766.89, 766.89]	1174.99 [1174.99, 1174.99]
XS_a	1072.31 [1061.59, 1083.03]	373.64 [369.9, 381.11]	100.00 [100, 109.2]	100.11 [100, 155.3]
XS_b	1189.80 [1166.01, 1201.7]	335.12 [325.07, 341.83]	478.62 [449.91, 513.41]	1500.00 [1365, 1500]
XFD_a	0.50 [0.5, 0.63]	0.50 [0.5, 0.68]	0.20 [0.2, 0.34]	
XFD_b	1.50 [1.47, 1.5]	1.50 [1.46, 1.5]	1.50 [1.47, 1.5]	
XFI_a		410.00 [391.5, 410]	410.00 [410, 410]	271.97 [108.79, 316.14]
XFI_b		791.10 [704.08, 800]	206.35 [202.22, 208.41]	763.83 [557.6, 800]
β_{PET}	554.52 [443.61, 730.25]			
β_{STD}		1065.45 [958.9, 1140.21]	548.22 [422.13, 641.11]	
μ_{pot}	169.23 [169.23, 169.23]	135.93 [134.57, 135.93]	160.79 [159.18, 160.79]	156.23 [156.23, 156.23]

(B)	Broad-leaved deciduous	Mediterranean broad-leaved evergreen	Mediterranean needle-leaved evergreen	Other needle-leaved evergreen
$XPET_a$	849.58 [813.61, 893.61]	501.47 [411.21, 555.38]	1065.24 [799.14, 1225.02]	872.37 [853.47, 882.92]
$XPET_b$	729.78 [649.51, 814.1]	983.49 [865.47, 1076.47]	1251.21 [1026, 1500]	314.85 [299.1, 336.88]
XTA_a	0.19 [0.08, 0.3]	1.16 [0.94, 1.43]	0.19 [0.12, 0.28]	0.52 [0.46, 0.55]
XTA_b	0.92 [0.68, 1.18]	1.99 [1.46, 2]	1.10 [0.93, 1.3]	0.62 [0.55, 0.74]
	[607.9, 800]	[272.07, 299.64]	[165.06, 207.83]	[270.52, 379.25]
$XSTD_a$	1880.04 [1861.24, 1931.24]	1324.24 [1311, 1363.97]	1539.57 [1524.17, 1539.57]	3167.35 [3135.68, 3199.02]
$XSTD_b$	1319.89 [1280.29, 1346.28]	858.25 [832.51, 866.84]	766.51 [758.85, 774.18]	2061.36 [2020.13, 2081.97]
XS_a	1300.00 [1287, 1300]	1300.00 [1287, 1300]	461.49 [456.88, 461.49]	376.70 [371.17, 384.24]
XS_b	780.69 [765.08, 788.5]	745.45 [730.54, 752.91]	195.10 [193.15, 199.66]	227.58 [218.48, 235.21]
XFI_a	409.10 [373.19, 410]	408.55 [401.38, 410]	338.54 [329.38, 348.69]	312.20 [291.22, 334.06]
XFI_b	715.17	289.43	179.42	318.26
β_{PET}	279.69 [195.78, 359]			
β_{TA}			0.03 [0.00, 1.00]	0.06 [0.01, 0.65]
β_{STD}			3.52 [1.5, 42.57]	251.28 [10, 300]
μ_{pot}	153.42 [148.82, 156.35]	193.53 [183.85, 197.79]	299.51 [296.51, 300]	129.64 [127.04, 132.23]
pz	0.79 [0.79, 0.8]	0.88 [0.88, 0.88]	0.69 [0.68, 0.69]	0.81 [0.81, 0.81]

(C)	Broad-leaved deciduous	Mediterranean broad-leaved evergreen	Mediterranean needle-leaved evergreen	Other needle-leaved evergreen
$XPET_a$	917.00 [885.98, 955.64]	400.00 [400, 428]	809.39 [793.01, 821.2]	974.83 [963.33, 974.83]
$XPET_b$	342.60 [304.91, 377.39]	533.47 [528.13, 551.33]	322.16 [309.27, 334.74]	312.66 [312.66, 325.16]
XTA_a	0.85 [0.79, 0.95]		1.50 [1.47, 1.5]	1.47 [1.41, 1.47]
XTA_b	0.80 [0.69, 0.87]		1.03 [0.99, 1.07]	1.35 [1.34, 1.42]
$XSTD_a$	723.52 [10, 2667.06]	839.93 [748.54, 873.53]		10.29 [10, 100.04]
$XSTD_b$	6438.42 [1995.91, 7000]	920.29 [883.47, 1041.88]		1343.20 [1249.17, 1456.33]
XS_a		100.00 [100, 116.8]	100.05 [100, 162.05]	286.09 [100, 1300]
XS_b		468.42 [435.63, 492.17]	519.55 [410.45, 629.94]	9982.27 [698.76, 10000]
XFD_a	0.20 [0.2, 1.07]	41.84 [3.95, 50]	3.09 [1.82, 4.24]	2.22 [2.18, 3.43]
XFD_b	0.63 [0.56, 0.67]	1.99 [1.83, 2]	0.63 [0.59, 0.66]	0.49 [0.49, 0.52]
XFI_a	147.22 [145.28, 152.48]	141.60 [123.28, 173.81]	56.39 [50, 69.83]	409.33 [402.14, 410]
XFI_b	70.01 [65.81, 72.93]	130.56 [90.09, 297.92]	313.07 [306.81, 335.67]	216.57 [216, 227.4]
β_{PET}				167.93 [0, 322.55]
β_{TA}				3.85 [3.7, 5]
μ_{pot}	4709.58 [4379.91, 4921.2]	4026.54 [3946.01, 4335.21]	5815.59 [5699.28, 6106.37]	7020.42 [7020.42, 7301.24]

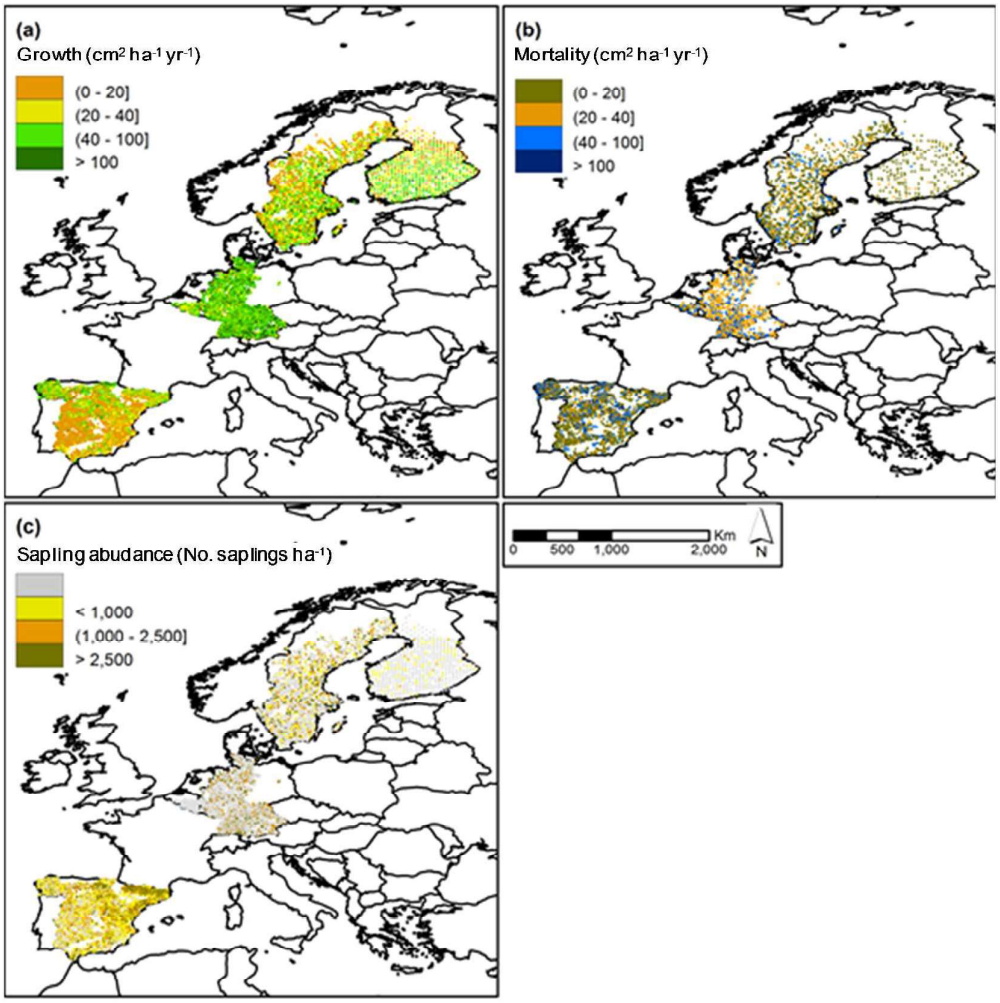

Fig. S1. Spatial distribution of the response variables in the National Forest Inventories included in the study: (a) tree growth (cm^2 ha^{-1} yr^{-1}), (b) tree mortality (cm^2 ha^{-1} yr^{-1}), and (c) sapling abundance (No. saplings ha^{-1}).

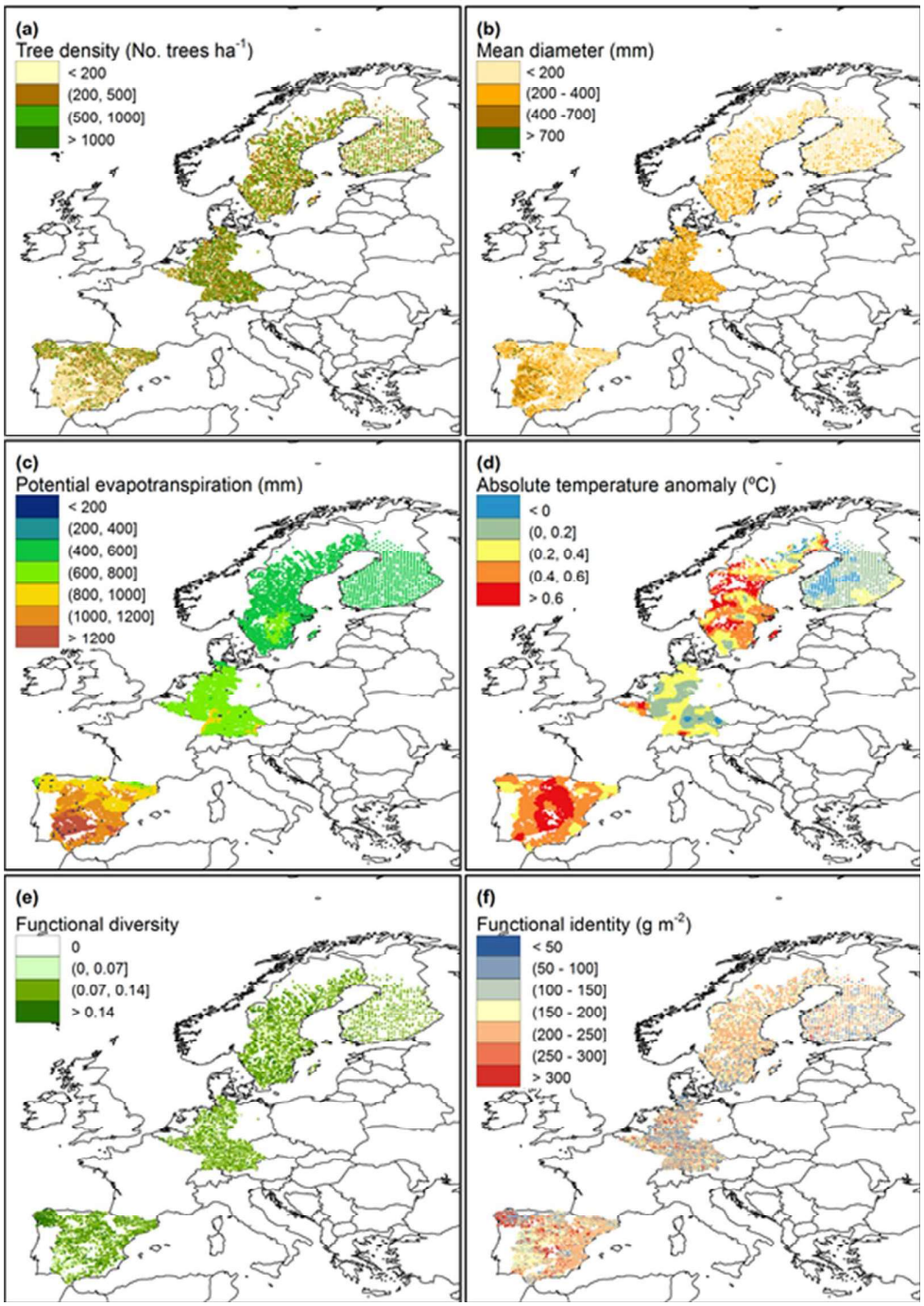

Fig. S2. Spatial distribution of the predictor variables in the National Forest Inventories included in the study: (a) tree density (No. trees ha^{-1}), (b) mean d.b.h. (mm), (c) potential evapotranspiration (mm), (d) frequency of dry years (ºC), (e) absolute temperature anomaly (ºC), (f) functional diversity (adimensional), and (g) functional identity based on leaf mass per area (g m^{-2}).

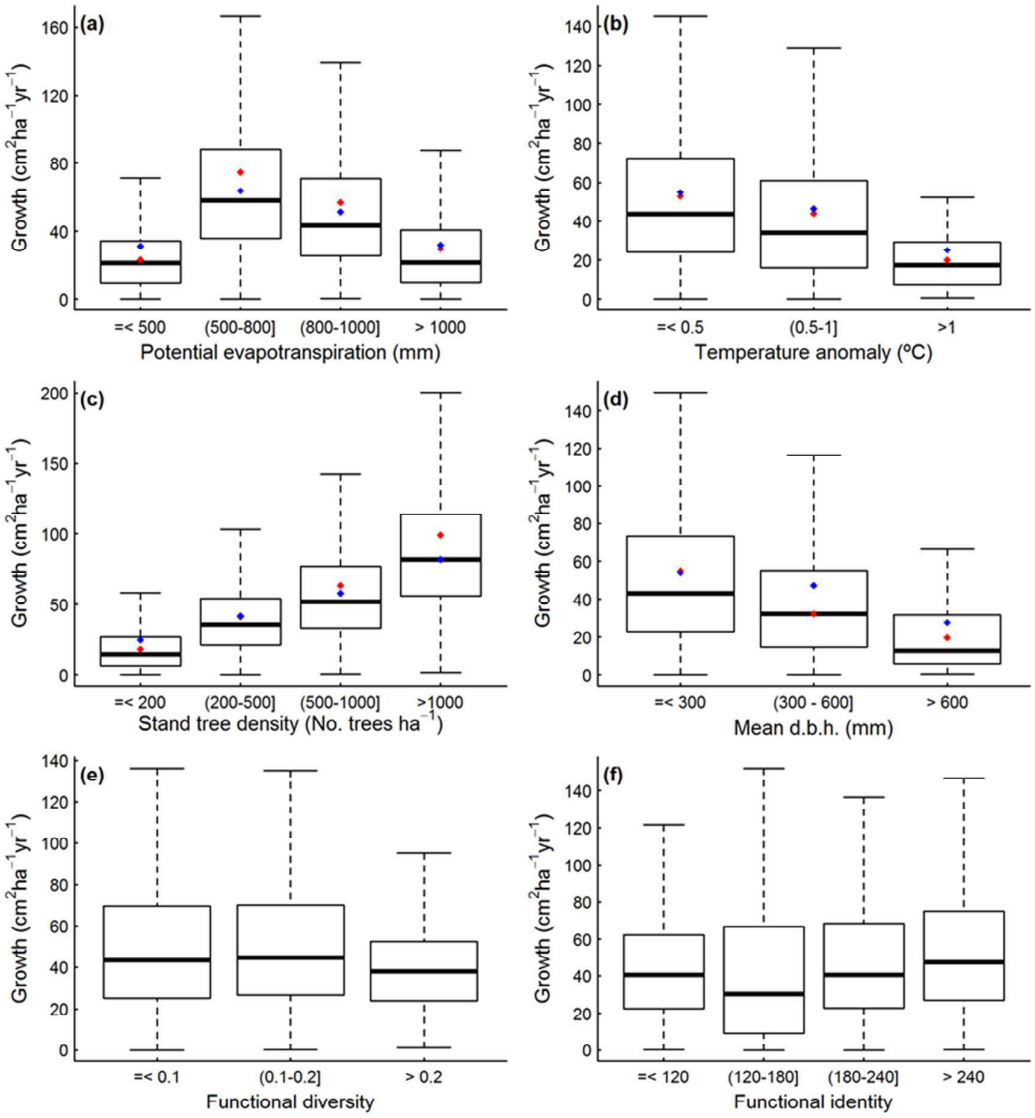

Fig. S3.1. Box-whisker plots of tree growth (cm^2 ha^{-1} yr^{-1}) along (a) potential evapotranspiration (mm), (b) temperature anomaly (ºC), (c) stand tree density (No. trees ha^{-1}), (d) mean d.b.h. (mm), (e) functional diversity (adimensional), and (f) functional identity based on leaf mass per area (g m^{-2}). Mean values are showed with dots in blue for mixed plots and in red for monospecific plots.

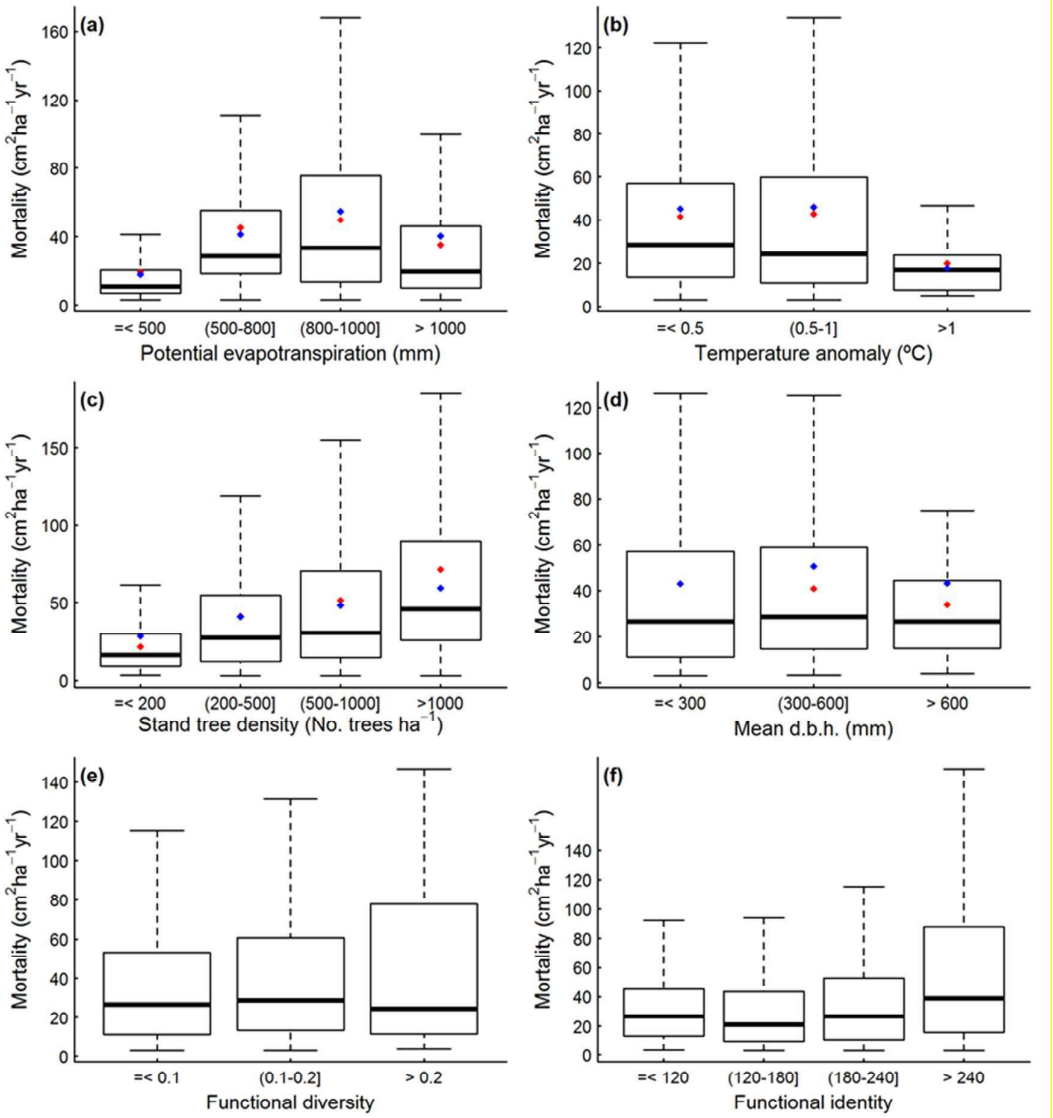

Fig. S3.2. Box-whisker plots of tree mortality (cm^2 ha^{-1} yr^{-1}) in plots where is larger than zero along: (a) potential evapotranspiration (mm), (b) temperature anomaly (ºC), (c) stand tree density (No. trees ha^{-1}), (d) mean d.b.h. (mm), (e) functional diversity (adimensional), and (f) functional identity based on leaf mass per area (g m^{-2}). Mean values are showed with dots in blue for mixed plots and in red for monospecific plots.

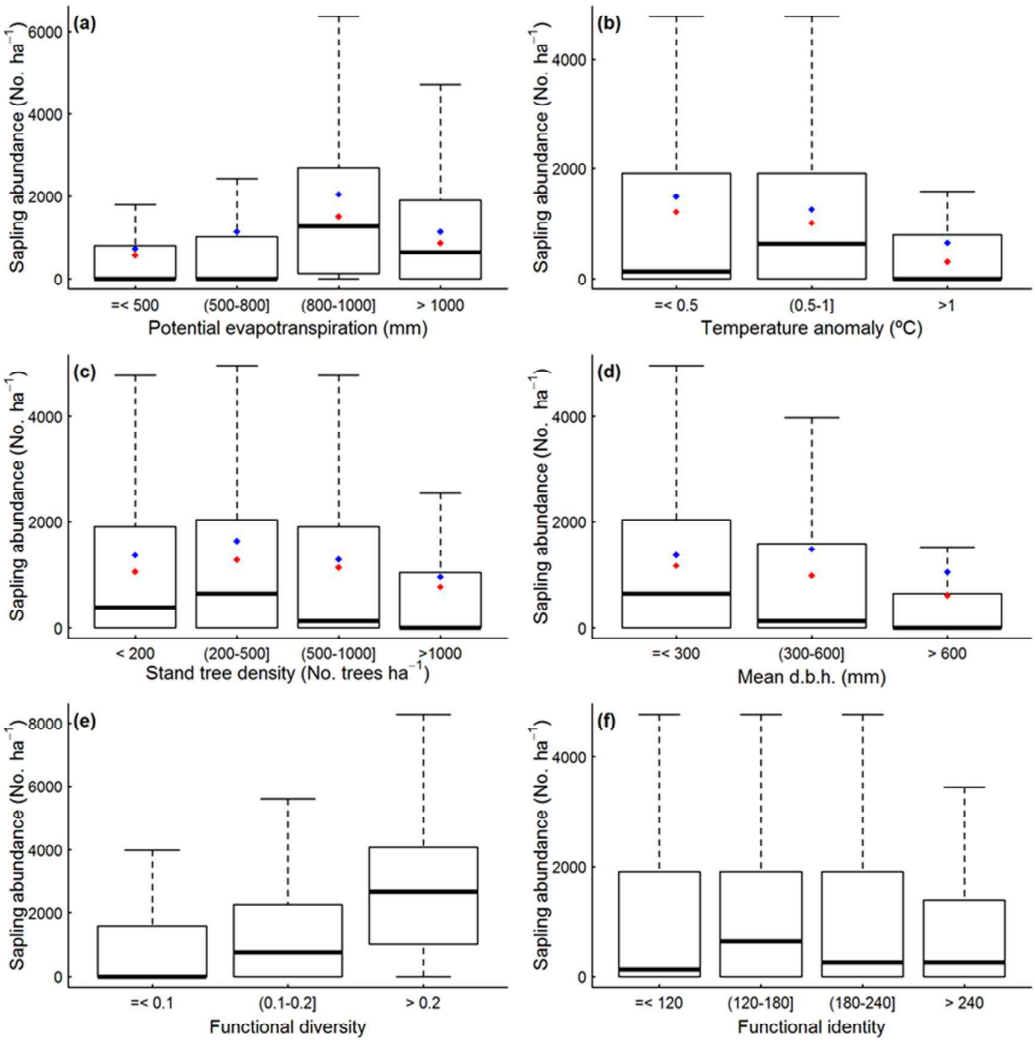

Fig. S3.3. Box-whisker plots of sapling abundance (No. saplings ha^{-1}) in plots where is larger than zero along: (a) potential evapotranspiration (mm), (b) temperature anomaly (ºC), (c) stand tree density (No. trees ha^{-1}), (d) mean d.b.h. (mm), (e) functional diversity (adimensional), and (f) functional identity based on leaf mass per area (g m^{-2}). Mean values are showed with dots in blue for mixed plots and in red for monospecific plots.

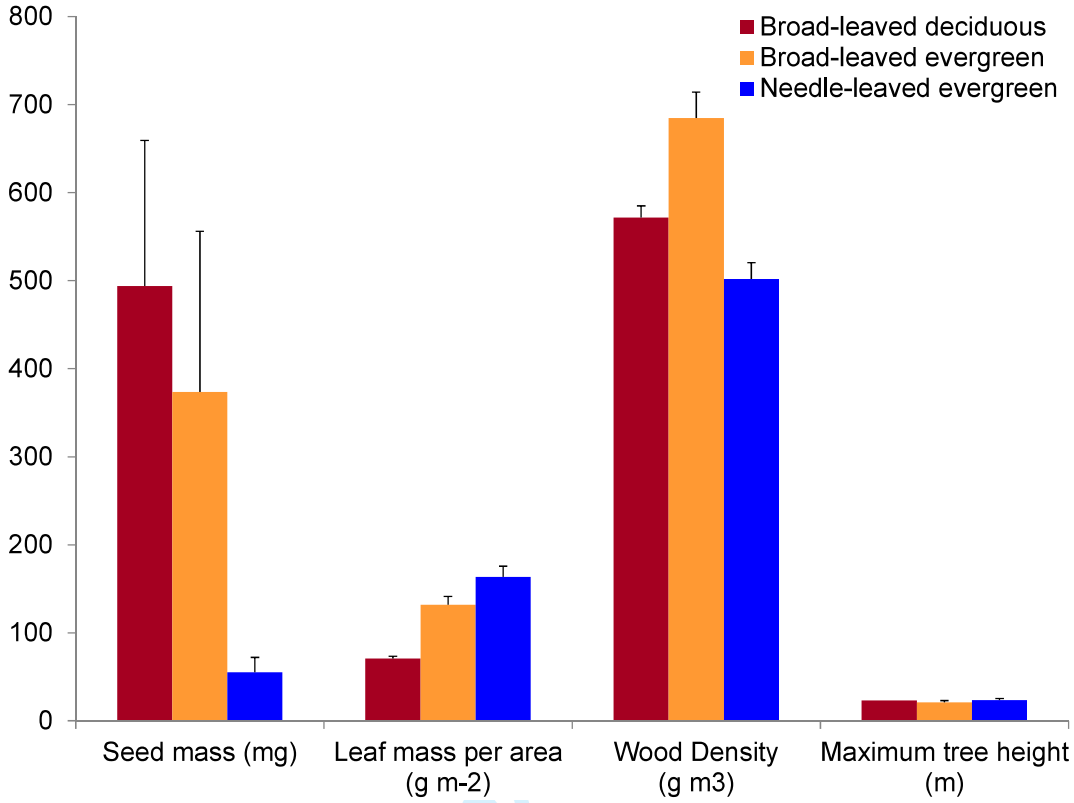

Fig. S4. Mean seed mass (mg), leaf mass per area (g m^{-2}), wood density (g cm^{-3}) and maximum tree height (m) depending on leaf characteristics used to define forest types (i.e. broad-leaved vs. needle-leaved and deciduous vs. evergreen).

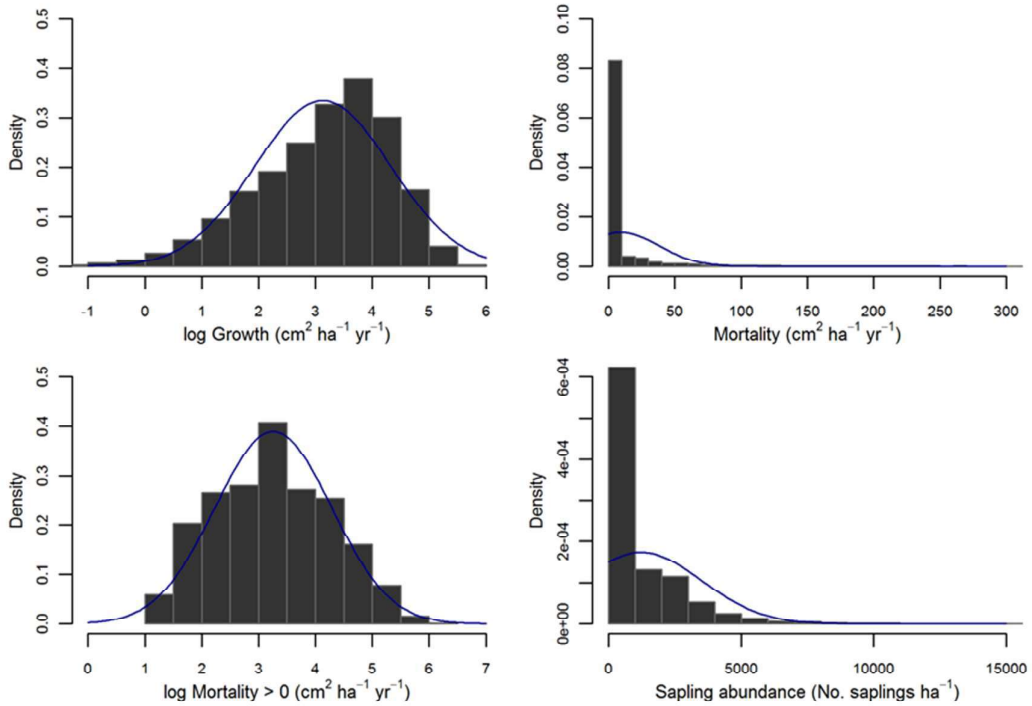

Fig. S5 Histograms showing the density distribution for tree growth (log Growth (cm^2 ha^{-1} yr^{-1})), tree mortality (Mortality (cm^2 ha^{-1} yr^{-1})), tree mortality larger than zero (log Mortality > 0 (cm^2 ha^{-1} yr^{-1})), and sapling abundance (No. saplings ha^{-1}).